Vol. 23 No. 1

January, 1957

THE BOTANICAL REVIEW

Interpreting Botanical Progress

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ON INSIDE BACK COVER

Published Monthly except August and September at
Box 749, Lancaster, Pa.

Entered as second-class mail matter February 4, 1935, at the Post Office at Lancaster, Pennsylvania, under the Act of March 3, 1879.

THE BOTANICAL REVIEW

Founded in 1935 by

HENRY ALLAN GLEASON and EDMUND H. FULLING

Managed, edited and published at
The New York Botanical Garden

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Articles are obtained primarily by invitation. Unsolicited manuscripts are also welcome. In all cases, however, the editor reserves the right to accept, reject or suggest revisions in submitted material. All manuscripts should be on double-space typewritten pages, with references and citations in accordance with the customary style of THE BOTANICAL REVIEW.

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All correspondence should be addressed to THE BOTANICAL REVIEW, at Box 749, Lancaster, Pa., or Fordham P. O., New York, N. Y.

THE BOTANICAL REVIEW

VOL. XXIII JANUARY, 1957 No. 1

THE INFERIOR OVARY. II[1]

GERTRUDE E. DOUGLAS
Feura Bush, N. Y.

INTRODUCTION

Reappraisals are the order of the day. They seem to be necessary not only in the political, but also in the botanical field, and they certainly can be agonizing! Ten years ago it appeared that the problem of the nature of the inferior ovary was fairly well solved, and that in the vast majority of families it is appendicular. There were some dissenters, however, and recently the validity of using the anatomical method in determining the nature of its wall has been called into question. Strange to our ears, indeed, are the statements that the problem of the inferiority of the ovary "is in most cases insoluble by anatomical evidence", and that the problem is "no longer of vital significance"—these by one who has contributed to this journal two excellent reviews in which the value of anatomical evidence in the solving of other morphological problems is demonstrated (1951, 1952b). One wonders whether Puri, in his enthusiasm for the new work on morphogenesis and histogenesis, has not lost sight of the importance of phylogeny in the consideration of morphological problems. "No longer of vital significance", indeed! Are these the words of a morphologist? Members of the anatomical school can not let this challenge go unanswered. Although most of the phylogenetic evidence upon which they have based their conclusions is not new, they feel that it should be restated. This the present author will attempt to do in the course of reviewing the literature of the last twelve years.

NATURE OF THE CARPEL

At the time of the previous review concerning the inferior ovary (1944), most botanists accepted the concept that the flower is the

[1] Supplement to article in The Botanical Review **10**: 125–186. 1944.

homologue of a short shoot consisting of a determinate stem bearing sporophylls. The carpel was regarded as the equivalent of an involutely folded leaf, the apex of which was transformed into a style and stigma. The ovules are borne on specialized marginal or submarginal areas, and are supplied with nourishment by lateral veins. This concept was held by most English, French and American botanists, but the German, Austrian and Swiss followers of Troll pictured the carpel as an asciculate, peltate structure bearing ovules on the "cross zone". Since that time, as the result of investigations of primitive dicot families, Bailey and Swamy (1951) have suggested that the old idea of the carpel needs modification. The most primitive one known (that of the Tasmannia section of *Drimys* in the Winteraceae) is a 3-valved, unsealed, conduplicately folded structure, with stigmatic area decurrent to the base, bearing on its upper or adaxial surface ovules that are nourished by both dorsal and lateral veins. Similar carpels are present in other primitive families, in some of which syncarpous tendencies have appeared and brought about lateral concrescence of carpel whorls as well as adnation of their margins to a central torus. Acceptance of the new view that the primitive carpel was of the *Drimys* type offers no obstacle to viewing the compound pistil as a syncarpous gynoecium, but old ideas of the nature of its placentae are in need of a change. The position of the ovules, as demonstrated in woody Ranales, is submarginal, not marginal. In primitive forms they are far from the edge; in advanced ones, close to it, but never on it. The placenta was originally a position only; in advanced types it has become an upgrowth of the ovary wall.

THE CLASSICAL THEORY AND ITS MODIFICATION

For those who had accepted the classical theory of the nature of the flower there were offered during the last 150 years a variety of theories concerning the tissues involved in the inferior ovary (Douglas, 1944). The most important ones were the following: it represents (*a*) a concrescence of the bases of the calyx, corolla, androecium and gynoecium, and is thus appendicular; (*b*) a hollow-receptacle, modified for reproduction, and is axial excepting for its carpellary roof; (*c*) a hollow receptable concrescent with a carpellary core; (*d*) an axial wall, containing a carpellary placenta. In types *a* and *b* the axis may penetrate the center as a

carpel-bearer. Research in floral anatomy carried on during the last century has led to almost universal acceptance of the view that the interior of the epigynous ovary is carpellary, but a divergence of opinion regarding the nature of the wall still exists. Many investigators, particularly those of Austria and Germany who have made their deductions from studies of ontogeny, still retain the axial-cup concept.

That an axial cup is present in a few genera—*Rosa* (Bonne, 1928; Jackson, 1934), *Calycanthus* (G. H. Smith, 1928), certain of the Cactaceae (Leinfellner, 1941; Sharma, 1949; Tiagi, 1955), *Darbya* and other genera of the Santalaceae (Smith and Smith, 1942a and b), *Carya* and *Annamocarya* (Shuhart, 1932; Leroy, 1955), though in the first two genera the ovaries are not truly inferior—has been demonstrated by the course taken by the vascular bundles in the wall. These bundles pass upward with xylem and phloem normally oriented, turn, proceed downward with vascular tissues inverted, and give off branches to the carpels near the base of the cup ("ovary"). The wall is regarded logically as receptacular to the point where the last carpellary ventral traces come off. If the turning downward takes place near the apex, a completely inferior ovary, as in *Darbya,* results; if it takes place half-way up, a semi-inferior ovary, or a perigynous cup, as in *Rosa,* comes about. Structures of these types are rare, however, and there is a large measure of concurrence among floral anatomists that the vast majority of inferior ovaries are appendicular, and that the wall represents a phylogenetic union of ovary wall and floral tube.

RECENT STUDIES OF MONOCOT GENERA

Recent studies of monocot genera have been few, but conclusions reached are mostly in agreement that the inferior ovary is appendicular. Wunderlich (1950) investigated Hutchinson's family Agavaceae from both ontogenetic and anatomical points of view. In a comparison of *Yucca* and *Beschorneria,* the former characterized by a superior, and the latter by an inferior ovary, she could find little difference. *Beschorneria* showed a higher degree of fusion at the base of the perianth, stamen and carpel bundles than did *Yucca,* but Wunderlich decided that the small amount of concrescence present in genera of the Agaveae is not sufficient to

warrant retaining the Yucceae and Agaveae as separate tribes, and placed *Yucca* in the Agaveae. The tribe Dracaeneae, however, in which the amount of adnation of the floral whorls is much greater, was maintained. The massive base of the ovary of this tribe owes its primary syncarpy to congenital fusion, whereas its upper part is secondarily syncarpous through postgenital unions. *Cordyline* was considered by her to be ancestral to the Dracaeneae, as well as to the Nolineae, in which similar congenital and post-genital fusions are present. She suggested that the terminus of the receptacle could be located fairly accurately in *Cordyline* at the groove that sets off the pedicel from the floral members. In regarding the carpels as peltate structures, she concurred with Troll, but she heartily took issue with him in his contention that the perigone of the Agavaceae is axial.

Wunderlich (1950) further stated her belief that a series of progressive adnations, as is present in the Agavaceae, can be duplicated in the Bromeliaceae. The same opinion had been expressed by Buchet (1928) in a reply to Bugnon (1926). Wunderlich questioned the conclusion of Leinfellner (1941), whose ontogenetic study of *Pitcairnia xanthocalyx* had led him to conclude that the wall consists of an axial cup. Baum (1948c) shared Leinfellner's views. She noted that the backs of the carpels of *Billbergia nutans* are fused congenitally with the axial cup, whereas the edges of the carpels and their flanks are united with each other through postgenital fusions.

The fruit of the bromeliad, *Ananas comosus,* has been thoroughly investigated by Okimoto (1948). Morphologically a pineapple is an inflorescence, the phylogenetic product of a high degree of concrescence of fruitlets, subtending bracts and inflorescence axis. During its evolution the flower cluster was subjected to so much compression and reduction that fusions took place, not only between bundles within the flowers, but also between the resulting compound cords and the veins of subtending or adjacent bracts. Remnants of all floral structures are present in the fruit.

The ontogeny of one species of the Taccaceae, *Schizocarpa plantaginea,* characterized by dry loculicidal capsules, has been studied by Kaussmann (1951). He interpreted the gynoecium as an axial cup lined with three strongly arrested carpels, congenitally united at the base, but free above, where the cavity be-

comes unilocular. The placentae are weakly developed on the carpel margins.

The family Orchidaceae, perhaps because of its high degree of complexity, was not studied with the aid of modern techniques until recently. Swamy (1948) has reported results of an extensive anatomical investigation of 40 species belonging to 20 genera. He concluded that the inferior ovary in all is an appendicular structure which has come about in the course of phylogeny through extreme adnation of floral whorls. The forces of connation, adnation and reduction, at work in varying degrees, have been responsible for the great diversity of spectacular flowers, within which, however, a basic vascular plan could be detected. The ancestral flower appeared to have been three-merous, with six sepal-like perianth parts, two staminal whorls, and a three-carpellate ovary having three functional stigmas. From such a flower the two main types which are characteristic of the sub-families, Diandrae and Monandrae, have diverged. In the Diandrae two lateral stamens of the inner whorl have remained functional, while one of the outer cycle has been transformed into a conspicuous staminode; all of the stamens and stigmas have remained free. In the Monandrae, on the other hand, the median stamen of the outer whorl has remained functional, while the lateral ones have been either lost (Ophrydenae) or compounded with other organs into the gynostemium, in which structure their traces are in more or less close union with those of the other whorl (in other Monandrae). The labellum is a highly developed perianth member with the typical vascular supply. The gynostemium, hitherto little understood, is interpreted as an appendicular, rather than an axial structure, since it contains the vascular traces of both staminal and stigmatic whorls.

RECENT STUDIES OF DICOT GENERA

JUGLANDACEAE

Turning now to the dicots and to the family Juglandaceae, the present writer regrets that one exceptionally important paper was overlooked in her previous review (1944). The report of Nast (1935), in which she followed the development of the flower of the English walnut (*Juglans regia*) from bud to maturity, is outstanding in its clear presentation of a complicated structure. Nast

attributed the inferiority of the ovary to adnations involving the involucre, perianth and two-carpelled pistil—a conclusion also reached by Manning for *Juglans nigra* (1926, 1940). She also cleared up some hitherto debated problems concerning the fruit. The husk consists of involucre and a thin layer of perianth; the shell, of the remainder of the perianth and the carpellary wall. The main septum is an outgrowth from the ventral edges of the carpels; the secondary partitions, developments from wall tissue opposite the dorsal sutures which grow inward at the top and base of the ovary, the upper one becoming split by the growth of the embryo. The two winged evaginations, which below the locule occupy the space between the elongated placenta and ovary wall, are placental outgrowths that function for a time as storage organs and break down. A single ovule is developed, but a double ovular trace indicates that the ancestral flower had two.

Inasmuch as an understanding of the floral anatomy of *Juglans* is necessary before the vascular system of the other genera in the family can be comprehended, it is necessary to go into some detail. Nast's figure No. 53 (Fig. 4), a diagram of a longitudinal section of a flower cut through the plane of the primary septum, will be of assistance. Three cycles of normally oriented bundles ascend from the stele of the pedicel into the bud, the outer becoming involucral traces; the middle, median carpellaries; and the inner, dorsal-ventral carpellaries. The latter cycle has an intricate history. Within the secondary plane four dorsal-ventral carpellary bundles, each consisting of a ventral and one half of a dorsal, come together in pairs and run upward within the ring of the second cycle, unfused, to about the level of C in the diagram. Here the ventrals leave the dorsals, turn inward and downward, becoming inverted in so doing; then, normally oriented again, they pass to the center. Within the primary partition, in the form of two semi-circular arcs, they run up to the winged evaginations, branch profusely, then become reorganized into four distinct bundles (H). Still within the primary septum they continue their ascent, two on each side, to about the level of the nucellus, where the bundles of each pair unite to form two ovular traces (G). The ovular traces become inverted and run downward, then, normally oriented, move to the center, and at the funiculus they fuse into a ring from which 12 integument bundles are derived. The two halves of each dorsal

bundle, left behind when the ventrals passed to the center, ascend in pairs to the apex of the flower, where they finally unite two by two, and enter the style. The whole picture is complicated by the branching and anastomosing of strands connecting the involucral with the perianth-carpellary system, and of the latter with the dorsal carpellary bundles.

Nast was not ready to commit herself regarding the nature of the tissue which bears the ovule—whether it represents carpel margins or a continuation of the axis. One fact favored the view that the "central column" is cauline; during ontogeny it appears slightly before the septum. On the other hand, in longitudinal sections of older flowers cut through the plane of the primary septum she found no trace of the column, and the ovule appeared to be borne on the united edges of the carpels. Also, she noted that the central system of bundles does not originate directly from the vascular cylinder of the pedicel, but from the dorsal-ventrals. Both of these facts favor the appendicular theory. Her labelling of the bundles of the central placenta "ventrals" would suggest that she did not regard the column as cauline.

Leroy (1955) has been engaged in making an extensive study of the family Juglandaceae, and has embodied his observations which have been appearing in numerous papers in recent years in a monograph. As an aid to his taxonomic work he made use of the vascular anatomy and ontogeny of flowers and fruits representative of eight genera. With only minor exceptions his accounts of the floral anatomy of *Juglans regia* and *J. nigra* agree with those of Nast (1935) and Manning (1926). The genera *Carya* and *Annamocarya,* however, reveal some surprising anomalies. When Shuhart (1932) reported the presence of recurrent bundles with inversely oriented xylem and phloem in the cupule of *Hickoria pecan* (*Carya pecan*), floral morphologists were inclined to be skeptical, for it did not seem possible that *Carya* could differ so greatly from its close relative *Juglans.* Manning (1926), however, had followed the course of the dorsal carpellary bundles of *Carya glabra* from the time they left the stele until they reached the style, and observed behavior similar to that described for the pecan by Shuhart. It is unfortunate that the part of Manning's thesis which dealt with the internal structure of the *Juglans* and *Carya* flowers was never published. Shuhart's find-

ings have been confirmed by Leroy (1951, 1955) and by a still more amazing anatomical situation discovered in the Indochinese species *Annamocarya sinensis* (*Carya sinensis*). Let us examine Leroy's longitudinal diagram of a young fruit, cut through the primary septum plane (Fig. 21). It will be noted that the middle cycle of bundles, consisting of recurrent, inversely oriented strands, as well as that of the innermost ring, the " placental bundles ", are contained within the shell layer. Excepting for the course which they pursue, however, their behavior is similar to that described by Nast for *Juglans*. Leroy concluded that both *Juglans* and *Annamocarya* belong to the same sub-family, and in *Carya* he found the connecting links. In the latter genus, however, the course of the recurrent bundles is not within the shell, but just outside of it, abutting the sclerenchyma of the husk; that of the inner cycle, the " placental bundles ", is always in the interior but varies in proximity to the wall. In *C. cathayensis* (Fig. 22) it is just inside the ovary wall; in *C. Poilanei* (Fig. 23) and *C. tonkinensis*, considerably nearer the center; in *C. cordiformis* (Fig. 24) and *C. pecan*, still nearer the center, but less so than in *Juglans*. In other words the " placental column " in its evolution seems to be either retreating from the shell to the center or broadening out from the center to the shell. Because of several primitive characters in *Annamocarya*, Leroy favors the former view but suggests that the problem needs further research. The series could be read in the other direction. Most interesting is the fact that the ovary of a young flower of *Annamocarya* is superior. It becomes inferior by the upward growth of a ring of intercalary meristem which produces the shell and unites the ovary with the peripheral tissues.

As the result of his studies of the juglandaceous flower, Leroy's conclusions contain some surprising negations. Strongly influenced by ontogenetic observations, he decided that its inferior ovary can not be regarded as cauline, appendicular or appendicular with a cauline placenta. The theory held by Benson and Welsford (1909) and Manning (1926) that the ovule is borne on the margin of carpels, as well as the belief of both Manning (1926) and Nast (1935) that the ancestral flower had at least two ovules, went into the discard also. Leroy called attention to the fact that the young flower of all three genera is produced by the growth of two

meristems; the one which produces the central column and ovule was considered to be homologous with the rib meristem of a vegetative shoot, and the other, from which the ovary wall and husk develop, identical with exterior axial meristem. It was impossible, he asserted, to distinguish leaf from stem. In consequence, the following theory was proposed: The juglandaceous flower is a qualitatively transformed vegetative shoot, a terminal ensemble which is both a vegetative shoot and a floral one. The zonal growth which produces it has "aspects" of both leaf and stem, between which there is no essential difference. "The methods at the disposal of the plant are inscribed in its heredity and determined by phyllotaxy", rate and change in the differential growth being influenced by both heredity and physiological factors. This conception was then extended to apply to all angiospermous flowers. It seems strange that an investigator who put so much emphasis on vascular anatomy in taxonomic work should have placed so little reliance on it in the interpretation of morphological structures. In his comparative studies of *Juglans, Carya* and *Annamocarya* (Figs. 21–24), the ascending bundles of the third inner cycle, "placental bundles", as he designated them, were considered to be homologous. In *Juglans* Nast (1935) and Manning (1926) have interpreted them as carpellary ventrals. Leroy, whether he likes it or not, has offered very good evidence for placing the placental bundles of *Carya* and *Annamocarya* in the same category. That would mean that the interior of the gynoecium of the last two genera is carpellary, as it is in *Juglans*. The nature of the husk, however, is another story. The ascending and recurrent cycles contained in the cupule indicate that it is axial, as Leroy (1951) pointed out in his earlier paper. The inferior ovary of *Carya* and *Annamocarya* appears to be of the *Darbya* type, whereas in *Juglans* it is appendicular, being the product of adnations of bracts, involucre and perianth with the ovary, as shown by Manning (1926, 1940) and Nast (1935), and earlier by Benson and Welsford (1909).

CACTACEAE

According to Puri (1952a), the axial cup type of inferior ovary was noted in certain species of Cactaceae by Sharma (1949), but his work was not sufficiently extensive to warrant publication.

At Puri's suggestion, a study of the morphology of the cactaceous flower was taken up by Tiagi (1955), who chose to work on the following species, representative of the three subfamilies—*Pereskia bleo, Opuntia dillenii, Mammillaria tenuis* and *Phipsalis cassuthe.* His anatomical work confirms the general opinion that the outer layer of the " ovary wall " is axial, a conclusion that can be hardly questioned, since flowers are often produced in the axils of the bractioles. The general course of the bundles is similar to that of *Darbya* and *Carya.* Normally oriented receptacular strands bend inward at the top of the " ovary ", give off traces to the perianth and androecium (and in *Pereskia* to the style), then become recurrent with inverse orientation. A peculiar feature of the flowers of this family is the lack of a third inner ascending ring which gives rise to the ovule traces. Here the funicular traces are derived directly from the recurrent ring. Tiagi thinks that the explanation for this unusual condition may be found in *Pereskia,* where an inner ring of weakly developed traces arises below the ovule region and a short distance above unites with the recurrent cycle. The recurrent bundles are apparently compound, having the ventral carpellaries incorporated within them. The ovaries are primarily unilocular but may become partitioned by secondary outgrowths from the placentae. Vascular anatomy confirms the general opinion that *Pereskia* is the most primitive genus of the family. *Pereskia bahiensis* was one of the species of which Leinfellner (1941) made ontogenetic and histogenetic studies, resulting in his conclusion that all inferior ovaries consist of peltate carpels sunken in hollow axes.

ONAGRACEAE

Three excellent papers concerned with the vascularization of the floral tube in certain species of the Onagraceae, illustrated by unusually clear three-dimensional diagrams showing the course of the bundles, have recently been published by Bonner (1948) and by Baehni and Bonner (1948, 1949). Bonner, who undertook his study hoping to find anatomical characters of value in the delimitation of species, reported that the floral plans of European species of *Epilobium* are almost identical, and that those of *Oenothera* and *Fuchsia* are similar to them. That of *Circaea* owes its slight differences to reduction. Since " the arrangement of the

floral vascular supply in *Epilobium* is such that the ovary wall can be regarded as of composite nature", Bonner looked upon the ovary as a superior one, "to the walls of which the basal parts of the outer floral whorls have fused". In two studies, in which the vascular systems of floral tubes of several onagraceous species were meticulously traced, Baehni and Bonner (1948, 1949) paid special attention to the section between the top of the ovary and the free segments of the perianth, where certain bundles end in weak tufts or glands. These are lateral branches of the exterior staminal-placental nerves, and were explained by the investigators as residual structures which once belonged to the summits of carpels now lost. A study of the vascular situation in the flower of *Lythrum Salicaria* suggested to them that the progenitor of the Onagraceae was similar to that of the less specialized Lythraceae. In their papers the authors commented on the inadequacy of the terms in current use applied to the inferior ovary: "receptacle", "hypanthium", "perianth tube", "calyx-tube", and even "floral tube". Bonner used "perianth tube"; and Baehni and Bonner, "floral tube". They should welcome the suggestion of Egler (1951), to be described later in this paper.

Olson (1953) made a study of early stages in the flower of another genus of the Onagraceae. He reported that during its development the flower of *Gaura coccinea* evolved from an early condition of hypogyny to that of "true epigyny". Since in the meristematic tissue that gave rise to the floral appendages he noted no fusions between petals and sepals, or between carpels and receptacle, he concluded that these organs never had been separate, and that the floral tube is solely the product of zonal development of a receptacular tube. He made no study of the vascular system, however, and must have read Wilson and Just (1939) carelessly, since he claimed that his conclusion was in agreement with theirs.

SANTALACEAE AND RELATED FAMILIES

Frank and Elizabeth Smith (1942b) followed the publication of their paper on *Darbya* (1942a), which was discussed in the previous review (1944), by another in which a report of studies of 24 other genera of the Santalaceae and closely related families was made. In all 40 species upon which they worked, the basic floral

plan is similar, although in some of the more highly specialized forms reduction has progressed to such a degree that it would be difficult to recognize it, were it not for intermediate forms. The Smiths were fortunate in having obtained material of *Darbya*. This genus (Fig. 5), in common with other more generalized ones, has two circles of bundles in the ovary wall, the outer with normal, the inner with inverse, orientation of phloem and xylem. At the top of the "ovary" the ascending bundles give off branches to the sepals or to the floral tube, then turn downward, and upon reaching the base branch and send out ventral carpellary bundles into the placenta. The stele is not completely used up in the process, and a small amount of "residual tissue" is left pointing downward and ending blindly in the pith. From this unusual behavior of the bundles Smith and Smith concluded that they are receptacular, and, in consequence, that the wall which contains them is receptacular also. Thus the apical cup which is fused to the ovary was regarded as an axis which had become invaginated in the course of phylogeny.

In some of the more highly specialized species of Santalaceae, the ascending and descending cylinders of stelar bundles are connected only by anastomoses; in others, a single cycle of amphicribral bundles is present. The latter bundle type indicates fusion of two vascular whorls, with consequent concealment of invagination. "Residual tissue" is generally present in the family. In the Olacaceae, generally described as having hypogynous flowers, Smith and Smith (1942b) noted the inception of tendencies toward both adnation of floral whorls and invagination of the receptacle. They concluded, therefore, that this family was ancestral to the Grubbiaceae, in which the gynoecium is appendicular, and to the Santalaceae, in which it is receptacular. The strongly reduced Loranthaceae and Myzodendraceae appear to them to have been derived from the Santalaceae. Fagerlind (1948) agreed with the Smiths' opinion that the Olacaceae has given rise to the Santalaceae, and suggested further that the latter family is the ancestor of the Viscaceae, Phorodendraceae and the Balanophorales, all of which have assumed parasitic habits.

A few other students have worked on the Santalaceae and their relatives. Rao (1942), whose paper appeared before those of Smith and Smith, concluded from an ontogenetical study of five

species that the central placental column represents a continuation of the axis because he had not been able to find within it any bundle connections with the main floral system. He did see, however, some isolated groups of vascular tissue within the placenta. These were noted also by Smith and Smith (1942b) in species which they regarded as reduced. Absence of vascular tissue, or vestiges of it, are typical of reduced flowers such as those of mainly parasitic genera, and the lack of vascular connections between placental remnants and other floral bundles is not proof that the central placenta is cauline. The flowers of the Santalaceae are generally regarded as highly reduced. Eames reports that when he and Wilson (1928) were studying the carpels of the Cruciferae they found that carpellary traces did not always appear until the fruit was partly developed. This they found to be true also of flowers of some related families, among them, the Capparadaceae.

Schaeppi and Steindl made morphological and ontogenetic studies of the two subfamilies of the Loranthaceae, the Loranthoideae (1942) and the Viscoideae (1945). Their conclusion was that the ovary wall, " as in all plants with inferior ovaries " consists of a concave floral axis, but that the placenta with which it is united is carpellary and " similar to that of the Primulaceae ". In a few forms they found evidence of a former syncarpous condition at the base of the ovary and under the stylar canal. The ovules, as well as the placenta, tend to become reduced, so that, as an end result, the embryo sac develops in the tissue at the base of the ovary (*Viscum*). Since this is a frequent condition in extremely reduced flowers, it is difficult to allocate to specific organs the tissue on which the ovules are borne.

CELASTRACEAE

The axial interpretation of the inferior ovary wall of the Santalaceae has been called into question recently by Berkeley (1953) who suggested that it is possible to explain all inferior ovaries as products of adnation. In the course of a study of the disk of the Celastraceae, he noted in *Euonymus atropurpureus* and *E. alata* a slight backward turning of the petal-carpel traces. This suggested to him that a more extensive development of this kind might have brought about the inferior condition in the Santalaceae as well as in *Rosa* and *Calycanthus*. He reasoned

thus: since in *Celastrus* and *Euonymus* the stele could be considered to terminate at the point of departure of the floral traces beneath the ovary, especially those of the carpellary ventrals, the bundles above this point could be regarded as appendicular, having been brought together in varying degrees of adnation. If the outer circle of ascending bundles in the wall of the ovary of the Santalaceae, *Rosa* and *Calycanthus* were to be considered as fusions of all floral members, and their recurrent extensions as unions of petaled and dorsal carpellary units, there would be no need for viewing the torus as an invaginated axis. It might better be considered as a highly reduced structure in which toral reduction and adnation of floral organs had concurrently occurred. He did not attempt to explain the residual tissue of the Santalaceae. The backward turning of the floral traces in *Euonymus,* emphasized by Berkeley, is of minor importance, however, for it is found in many strictly hypogynous flowers. Copeland's (1943, 1947) and Palser's (1951, 1954) excellent diagrams of ericaceous flowers come to mind at this point. Widening and flattening of the receptacle naturally brings about this bent course of the outer appendage veins; they doubtless represent first steps in the evolution of an evaginated apex. Berkeley, however, has noted processes which take place in the development of an appendicular inferior ovary. The semi-inferior condition present in *Euonymus* and *Pactistima* is the result of fusion of stamen, petal and sepal bases with the ovary.

Rao (1949) reported that the perigynous calyx tube of the family Turneraceae which contains the bundles of sepals, petals and stamens is fused with the ovary at its base. Because of this concrescence, the ovaries of this family can be considered to be truly semi-inferior, as are those of *Euonymus* and *Pactistima.* The distinction between true semi-inferior ovaries and perigynous cups has not always been made.

BEGONIACEAE

New light has been brought to the problem of the inferior ovary of *Begonia,* which had been an issue between Bugnon (1926, 1928a, b) and Saunders (1925, 1927, 1931). Gauthier's very thorough comparative study of five species makes it clear that the interpretation of classical morphology (by far the simplest one)

can be retained. The inferior ovary is appendicular, composed of three seven-veined carpels congenitally united with the floral tube, the perianth of which may consist of six, five or two members. In a cross section of the ovary (Fig. 8) there is noticeable in each wing a large compound cord and two bundles with their xylem regions facing each other. In each flat side there is a still larger cord. The components of the large vein in the angle of each wing are a dorsal-sepal and dorsal-carpel bundle; of the cord in the flat side, two sepal bundles, two outer carpellary laterals (marginals) and a pair of ventrals, each of which belongs to an adjacent carpel. The two smaller bundles which face each other in the wings are inner carpellary laterals (medians). The various constituents of the compound bundles separate from each other at the top of the ovary. The situation is complicated, however, because in some species, including *B. octopetala* (Fig. 7), the prominent dorsal-sepal-dorsal-carpel nerves of the wing angles disappear temporarily in anastomoses near the top of the ovary. They reappear intact at the top and then separate, one of each pair entering a sepal, and the other continuing into the style. In *B. socotrana* (Fig. 6), on the other hand, the large dorsal nerves do not anastomose, but continue unbroken to the style. The unilocular condition and parietal placentation in the upper part of the ovary of some forms is made possible by the union in pairs of ventrals belonging to adjacent carpels. Gauthier noted a small amount of residual tissue in the base of the ovary of *B. octopetala,* just above the point where the pedicel begins to enlarge. This indicated to him the terminus of the receptacle. Reduction has been so extensive in some forms that interpretation of their anatomical structures is extremely difficult. It was on one of these forms that Bugnon worked. *B. socotrana* contains the key to the solution of the problem, and Gauthier was fortunate in having chosen it for study. Saunders might have come to a correct conclusion had not her interpretation been warped by her false theory of polymorphism.

Bugnon has not accepted Gauthier's conclusions and is clinging tenaciously to his opinion that the wall of the inferior ovary is axial. In a particularly bitter paper, written in collaboration with his son (1953), an attempt is made to show that Gauthier's work, " based on anatomy conjectured up by A. J. Eames ", is of purely

descriptive value. "En définitive, toute l'argumentation de R. Gauthier ne s'appuie que sur des critères sans valeur, des affermations sans preuve, des hypothesès sans fondement"—hardly the words of objective scientists! Their arguments are the same as those advanced by the senior author in previous papers (1926, 1928a, b), and there is no report of work on additional species. The paper contains an exposition of various aspects of vascular cylinders of stems at the nodes, where ramular and foliar gaps and segments are very complex, and are often confluent. The authors see in the vascular bundle pattern of the inferior ovary wall a striking similarity to that of a dissected siphonostele at a node; thus the loci where the bundles separate from each other are regarded as nodes that have been elevated to the top of the ovary by intercalary growth. Bugnon and Bugnon cite a paper of Arnal and Loiseau (1946) on *Tropaeolum majus* to show that it is possible to place the origin of an appendicular trace in a plexus. When this reasoning leads to the conclusion that the spur of a nasturtium flower is an axial structure, one wonders how it can be taken seriously and used to overthrow the solidly founded reasoning of Gauthier, whose paper presents a thorough and comparative study of the anatomy of the genus as a whole. Furthermore, the criteria which Gauthier used are not the propositions of a single school of thought, but those which have been broadly accepted by morphologists and taxonomists. Gauthier's paper has been generally welcomed as an outstanding contribution to the floral morphology of an important family.

More logical are the arguments of Leinfellner (1954), who compared the venation patterns of bracts and perianth segments of staminate and pistillate flowers of *Begonia heracleifolia.* Because he noted close similarity between the veining of bracts and tepals, not only in each sex but also between homologous structures of both male and female flowers, he concluded that these findings furnish additional evidence for believing that the wall is axial. Since, however, in working out homologies of foliage leaf, bract and tepal of other species, he had observed that the basal parts of all appendages have undergone extreme reduction, it might be countered that a similar process had gone on in *Begonia.* The bases of the male tepals may well have been lost in the process of

evolution, whereas their counterparts in the female flowers have not done so because of their concrescence with other floral whorls.

MELASTOMACEAE

The last dozen years have witnessed an increasingly greater use of comparative morphological and anatomical data in taxonomic work to supplement that derived from other sources. In general this has proven to be of greater diagnostic value when applied to genera and larger groups than to species. In the genus *Mouriri* and other genera of the family Melastomaceae, Morley (1953) found, not only some unusual and fascinating anatomical variations, but also characters that were of importance in the regrouping of species into subgenera and of closely related genera into tribes. At first glance one might think that some of the highly specialized species of the genus have receptacular ovaries such as are present in the Santalaceae, but a comparative series shows that they are clearly appendicular (Figs. 9–12). Differential growth has caused the central parts to shift downward, the lower parts outward, and the outer parts inward, naturally bringing about great changes in the vascular pattern and form of the placenta. Accompanying reduction of the locules and number of ovules, some bizarre types have been developed that bear little resemblance to the ancestral flower. It is the view of Morley that the progenitor of the group was similar to the existing *M. truncifolia* (Fig. 10), in which the inferior ovary has an axile placenta upon which are borne many ovules.

ARALIACEAE

Two species of the Araliaceae have been recently studied. In *Hedera helix* the inferior ovary is a product of the adnation of non-vascular tissue only. According to Eames and MacDaniels (1947), "the traces of all adnate organs run free to the base of the ovary in the positions they would have if there were no fusion". In *Hedera nepalensis,* studied by Singh (1954), the sepal, stamen and carpel traces, as well as the petal and carpel traces, are undiverged up to the top of the ovary. Singh reported that the vascular pattern of this flower is similar to that of *Acanthopanax suboldianum,* studied by Saunders, but he did not subscribe to her theory of polymorphism.

CORNACEAE AND CAPRIFOLIACEAE

Vascular anatomy of the flower of the Cornaceae and of the Caprifoliaceae has been the subject of recent studies by Wilkinson (1944, 1948a, b, c, 1949), and these have made important contributions to the taxonomy of the two families. The inferior ovary of both is appendicular, but each is characterized by a different type of placentation. In the Cornaceae it is fundamentally parietal, whereas in the Caprifoliaceae, fundamentally axile. Within the Cornaceae (1944), in spite of the striking similarity of the external forms of various species, a surprising number of variations occur in their vascular anatomy. Bundles in the wall of the ovary are made up of different combinations of gynoecial strands with those of sepals, petals and stamens. Wilkinson postulates the ancestral flower as having been five-merous. During the course of evolution the number of perianth parts has been reduced to four, and of carpels to two. This naturally has brought about a shifting of position of the vascular units as well as some unusual fusions. The pairs of ventrals, the members of which belong to adjacent carpels, do not enter the septum, a behavior which suggests that the original placentation was parietal. The septum itself owes its origin to the extension and union of placentae, not to the fused edges of the carpels.

In the Caprifoliaceae, on the other hand, Wilkinson (1948a, b, c, 1949) noted that the basic placentation is axile, and that the parietal form, when it occurs, is derived from it. Tendencies toward fusion, reduction, abortion of ovules, distortions of tissues, proceeding at different rates, have brought about a very great number of anatomical modifications of specific value. Adnation has gone so far in the tribe Lonicereae that pairs of flowers with inferior ovaries on opposite sides of the stem are fused. Remnants of the tips of inflorescence axes may persist in the fruits. In such flowers the pedicel anatomy of different species shows stages in stelar fusion ranging from two separate steles through two semicircular arcs to a single stele. The sterile necks of the fruits of many species have been produced by the abortion of ovules and closing of the locules. The tribe Linnaeae and the genera *Sambucus* and *Triosteum* have axial placentation and both multiovulate and uniovulate carpels. The specialization of *Viburnum* is

extreme, and its vascular anatomy would be difficult to interpret were it not for more primitive forms. A large excentric locule, united with two abortive ones beside it, contains a single ovule which does not belong to the carpel that forms it, but to the placenta common to the two abortive carpels (Figs. 15–20). The apparently fertile carpel is sterile: one of the two apparently sterile carpels is fertile. Truly nature is wonderful!

Arnal (1948), from observations made during an ontogenetical study of *Sambucus,* reported that there is an "incontestable discontinuity" in the appearance of the procambium of the median nerves of petals and carpels, and that its development was basipetal and basifugal from these loci. The points at which differentiation began were less evident in the other floral bundles, but they generally could be detected. From this he drew the conclusion that the cambium-initiating positions indicated the limits of stem and leaf. Since these limits are naturally located at the level of the insertion of floral parts of the receptacle, he argued that one could rightly consider that the lower part of the ovary, situated below the loci of insertion, is axial. This would mean that carpellary leaves are present in the inferior ovary only in its upper part—a conclusion reminiscent of the old Schleiden hypothesis. But, as will be noted later, discontinuity in procambium development in floral organs has been rejected by most of the recent investigators of apical meristems.

RUBIACEAE

One species of the family Rubiaceae shows an involvement of the tip of its inflorescence in its fruit similar to that noted by Wilkinson in *Lonicera.* In *Mitchella repens* Blaser (1954) found varying degrees of union between pairs of flowers coming from opposite sides of the stem. In some of these two-flowered clusters, in which their inferior ovaries are united but their perianths widely separated, the fusion is confined to the non-vascular tissues of the ovaries. Two steles (Fig. 13) are present in the peduncle, and the traces diverge to each flower in a symmetrical pattern—with more or less extensive unions taking place between bundles lying in the same radii within each flower. The majority of the two-flowered clusters, however, have a common stele (Fig. 14), and their vascular bundles are amalgamated and reduced in num-

ber. The fusions are not limited to bundles which lie in the same radii, but laterally adjacent ones are brought together, and bundles from two flowers fused. This account recalls the situation described for *Ananas,* where Okimoto found some of the bundles of an ovary united with those of adjacent flowers and bracts and with the subtending bract. In Blaser's material three- to four-flowered cymes, in which remnants of vestigial leaves were present, occasionally turned up. The inclusion of the floral apex in the fruits of such flowers led Blaser to infer that the precursor of the *Mitchella* was a several-flowered dichasial cyme.

COMPOSITAE

As is well known from the work of Koch (1930) and others, considerable variation has resulted from reduction and concrescence of the flowers in the Compositae. Snow (1945) studied the flower of *Chrysothamnus nauscosus speciosus* and concluded that the floral tube is not an invaginated axis, but a structure composed of the undiverged basal parts of the flower. In her words: " Certainly there is in *Chrysothamnus,* as well as in other Compositae, considerable zonal growth of all parts up to the top of the ovary . . . and of the petals and stamens for a considerable distance above that level ". Kasapligil (1951), in an ontogenetic and morphological study of *Umbellularia californica,* observed that the zonal growth which is responsible for producing the short perigynous tube occurs in the common bases of sepal, petal and the staminal primordia. Stebbins' (1940) observation of a lack of union between the ovary and floral tube bundles in the genus *Dubyaea,* of the Cichoriae, is interesting in this connection. He suggested that the tribe has not advanced far beyond the superior ovary stage. Massive zonal growth, then, does not necessarily mean extension of the receptacle.

PURI'S CRITICISM OF THE APPENDICULAR THEORY

Puri's criticism of the commonly accepted appendicular theory of the inferior ovary was first voiced in his comprehensive review, " The role of floral anatomy in the solution of morphological problems " (1951), published in this journal. It was later expanded in his " Floral anatomy and inferior ovary ", in " Phytomorphology " (1952a), accompanied by diagrams which are

certainly needed for an understanding of his concepts. Citing Eames (1931) and Gauthier (1950), Puri (1952a) readily admits that the inner part of the organ is truly carpellary, but he holds that the composition of the wall is impossible to determine in many cases because anatomists have left out of account the receptacular cortex through which the floral bundles, as traces, must pass before entering external organs. Zonal growth occurring in the deeply seated region might push the external organs upward, and thus form a wall, receptacular in nature, whose limits would be difficult to determine. Three types of ovaries could be produced, depending on where the zonal growth takes place. Photographs of Puri's diagrams are reproduced in Figures 1–3. If (as in Fig. 1) it is most active in the extreme peripheral region of the receptacle, and thus involves only the bases of the floral organs, the cup is largely carpellary; if (as in Fig. 2) it is most active in the middle layers, just outside the region where procambium tissue differentiates, it would be receptacular; if (as in Fig. 3) it is most active in the inner side of the region where procambium develops, the cup would also be receptacular, but of the *Rosa, Calycanthus* type. He thinks that type 2, intermediate between the others, has not been conceived so far, but it seems little different from the "growth *en masse*" concept of Coulter (1910), and others of his school, among them Kraus (1913), Kraus and Ralston (1916), Black (1916), Turkey and Young (1942).

Puri (1952a) admits that in type 2 the bundles of the wall are appendicular, "as was shown by Eames (1931), and confirmed by Gauthier in *Begonia* (1950)". He thinks, however, that the nature of the bundles is not the key to the problem, "for we know that leaf traces arise in stems at considerable distance below the leaf, in tissues which are clearly not leaf tissue". "The nature of the inferior ovary is, in my opinion, a part of that ever-insoluble (?) problem as to where the axis ends and the leaf begins. We cannot help stating that modern studies have deprived the terms, 'axis' and 'leaf', of much of their morphological significance (see Arber, 1950). They are merely descriptive terms, which serve for convenience more than anything else". "The present author no longer regards it of any vital significance".

Puri's arguments run as follows: if the inferior ovary is always appendicular, "either (1) there is no receptacular cortex in the

region of the floral appendages, or (2) if the cortex is present, the growth which brings about the inferior position of the ovary is confined to the extreme peripheral region adjoining the bases of the sepals, petals and stamens, and never involves the internal or deeper layers". Involved in the first assumption is the "so-called principle advanced by van Tieghem (1871) that 'the differentiation of a floral part begins at the point where the vascular bundle leaves the stele'. A necessary corollary of this will be that the vascular bundles, as soon as they separate from the parent stele, begin to traverse the tissue for which they are intended, that is there is no cortical tissue between the floral appendage and the stele of the receptacle". MacDaniels (1940), "who held such a consideration as valid" in his study of the apple, comes in for adverse criticism. "It is no longer possible to believe in the out-of-date statement of van Tieghem, much less base our conclusions on that". Puri's reason for so thinking is largely based on "overwhelming data, derived from modern work on development and histogenesis, which go to show that floral organs like foliage leaves are initiated by periclinical divisions in the peripheral layers (tunica) of the axis". Further, he could find no statement "worth our notice, on record, where the floral leaves were shown to be initiated in deeper layers where the procambium differentiates", although he did admit that some work went to show that leaf traces determine the leaf. Wardlaw's recent work on morphogenesis, which indicates that traces to organs differentiate as the result of basipetal movement of metabolites from active apices of these organs, seemed to him to clinch the matter. "Further, it has been claimed that the procambium in the developing carpel of *Amygdalus* appears first in the central part of the primordium, and only afterwards becomes connected with the vascular system by basipetal extension (Brooks, 1940). Such a condition is reported to be quite common in angiosperm leaves (Nast, 1944; Philipson, 1949; Sifton, 1944; Grégoire, 1938). If this, as it seems likely, turns out to be a more general condition, it will deal another serious blow to van Tieghem's conception".

In regard to the second assumption, that the growth which brings about the inferior ovary is confined to the extreme peripheral layers, he insists that it is difficult, if not impossible, to prove, since it could take place in deeper and inner layers, as

shown in his diagram of Fig. 2. " It was perhaps lack of appreciation of this possibility that led MacDaniels (1940, p. 20) to argue that ' if the pome flowers were in part receptacular in nature, a doubling back of the stelar bundles supplying the carpels would be expected, as is the case with *Rosa* and with *Rubus odoratus* '". Puri concluded, therefore, that " it is obvious that in Figs. 1 and 2 the vascular ground plan will be practically the same and it will be very difficult, if not impossible, to distinguish between the receptacular and appendicular 'cup' merely on the basis of anatomy. It is true that in both these cases the vascular bundles are appendicular, rather than stelar. But, as has already been pointed out (Puri, 1951), it must be remembered that an appendicular bundle has a dual character: *it is a ' trace ' when it traverses the cortex of the receptacle and ' bundle ' when it enters the organ.* Now we have no easy means of distinguishing where one ends and the other begins. Hence vascular anatomy can help us little in solving the problem of the inferior ovary in cases similar to those shown in Figs. 1 & 2".

It must be admitted that at first glance Puri seems to have presented an air-tight case, but careful study of his arguments reveals rifts in the lute. Granted that recent studies of floral organs, as well as of leaves, have shown that initiation of their primordia generally takes place in the second tunica layer, it frequently begins in the corpus, and even when cell divisions start in the tunica, others occur simultaneously, or immediately following in the corpus. According to Gifford (1954), foliar initiation ensues in the second layer of the tunica in about 64% of the angiosperms. In the remaining 36% there are many reports of corpus initiation. Participation of the corpus with the tunica in the origin of leaves has been reported by an imposing number of rencent workers, among them the following (and the list is not complete): Ball (1950), Boke (1947), Cross and Johnson (1941), Engard (1944), Esau (1943). Gifford (1950, 1954), Gunkel and Wetmore (1946), Hsü (1944), Leden (1954), Millington and Gunckel (1950), Popham and Chan (1950), Sharman (1945). Further, the limits of tunica and corpus are often unstable, even in the same plant (Ball, 1950; Eames, 1947; Esau, 1943; Foster, 1949; Gifford, 1954; Miller and Wetmore, 1945; Ozenda, 1949; Philipson, 1949; Tepfer, 1953).

There have been fewer researches on the initiation of floral primordia, but the consensus of modern opinion is that it also is not exclusively a tunica function (Boke, 1948; Engard, 1944; Leinfellner, 1941; McCoy, 1940; Philipson, 1949; Sass, 1944; Satina and Blakeslee, 1941, 1943; Tepfer, 1953). In the words of Popham and Chan (1950), "tunica and corpus are at best topographical terms and indicate nothing as regards ontogeny". Foster (1949) stated that the question of whether a structure is axial or appendicular can not be resolved by determining in which layer or layers of the shoot it originates. Furthermore, the procambium makes its appearance early, in close proximity to the primordium of its organ, and, in the words of Esau (1953), "it is now apparent from many recent studies of growing points that the newly developed cells are above and in contact with those that have appeared earlier". In other words, the procambium differentiates acropetally (Leroy, 1955; Philipson, 1949; Wetmore and Wardlaw, 1951). Grégoire's conclusions have often been shown to be without value. Development in two directions seems to be confined to the traces which connect late-appearing buds with the bundles of the axis. It would seem that Puri has been hasty in assuming that the van Tieghem hypothesis has been rendered out-of-date by these studies. The initiation of floral leaves, although relatively superficial, does extend inward more deeply than he has assumed, and is even continuous with the cambium in many cases.

Regarding the work on morphogenesis, it has been clearly established from the experiments of Ball (1949, 1950), Wardlaw (1950, 1953) and Wetmore and Wardlaw (1951) that the plant apex is an organizing center which influences the development of tissues beneath it. Whether or not the leaf primordium determines the inception of the procambium strand or whether the strand, continuous with the vascular system below, determines the leaf is still a problem concerning which specialists disagree. In Wardlaw's words (1953), "There is good evidence that the inception of the vascular tissue is directly due to the activity of shoot apices—the effect being a basipetal one. The actual progressive differentiation of the vascular system is in the main acropetal". At the Seventh International Botanical Congress in Stockholm, Esau (1950) suggested "that the pattern of vascularization is determined not by the apical meristem alone, and not by the mature

axis alone, but by the different parts of the shoot". In either case, the present writer is at a loss to see how the method of procambium inception would affect the tenability of the van Tieghem hypothesis, for growth is a physiological process taking place in the ontogeny of the shoot and the flower.

One of the conclusions reached by Wetmore and Wardlaw (1951) is that their results "set aside any possible adherence to the phyton concept, the view that the primary body of a vascular plant is an accumulation of units, each consisting of a leaf and its subjacent segment of stem". They believe that a stele is clearly present in the axis of ferns and other vascular plants. Notwithstanding Puri's opinion that "modern studies have deprived the terms 'axis' and 'leaf' of much of their morphological significance", the experiments of Wetmore and Wardlaw would support the view that concepts of leaf and axis can still be retained, irrespective of phylogenetic history. In spite of the many remarkable changes in meristems which Wardlaw was able to make, he never changed what was visibly a leaf primordium into a bud (Wetmore and Wardlaw, 1951). Even though in ancestry the leaf was a partial shoot, an aggregation of telomes or an innation from an axis, it did reach the evolutionary stage of appendage nature, similar to its modern form, many millions of years ago. The present writer is again reminded of the statement of Scott (1932) regarding floral leaves: "In Pteridosperms the reproductive organs are borne on appendages fully differentiated as leaves. No doubt both fertile and sterile portions were thallus branches, but in the Pteridosperms they have become obviously foliar. To call the fertile portions branches or branch systems seems an anachronism! They were no longer that in the Pteridosperm stage". The work of Foster (1949) and his students Tepfer (1953) and Kasapligil (1951) has confirmed the theory that all types of appendages, cataphylls, prophylls, bud scales, floral bracts and floral appendages are homologous with foliage leaves.

VALUE OF COMPARATIVE ANATOMY IN DETERMINING PHYLOGENY

That the van Tieghem hypothesis is rendered out-of-date by modern studies does not seem to be proven by Puri's arguments, but, even though it were, the use of vascular anatomy in determin-

ing the nature of the inferior ovary has a sounder basis. It should be emphasized that studies in histogenesis and morphogenesis are concerned with the ontogeny of the flower, whereas comparative vascular anatomy deals with its phylogeny. The law of biogenesis holds good for the plant, as well as for the animal, but only in a general way. We should not expect to find in the development of a modern flower growth patterns which exactly duplicate those which have taken place in the past, although some seem to occur. The place of origin of a primordium, the initiation and direction of growth of the procambium, as well as the region where more or less active growth takes place in the floral apex, are concerns of maturation and do not necessarily recapitulate stages which have taken place in the evolution of the flower. According to Esau (1953), "the ontogenies of plant parts are known to undergo phylogenetic changes. Therefore it would seem that developmental studies would contribute most to the understanding of the flower, if they were combined with studies of plant anatomy. Furthermore, both kinds of studies should be carried out along broad comparative lines". It is on broad comparative lines that the researches of the anatomical school on the inferior ovary have been carried out.

Since countless reductions have occurred in the evolution of an inferior ovary, it is fortunate for us that the stages through which it has passed are often revealed by flowers of closely related plants which have lagged behind in their advancement. With very few exceptions, the vascular skeleton can still be regarded as the most conservative of all systems in the angiosperms. Puri admits that it is of great value "when used judiciously". Why it is not judicious to use it in explaining the inferior ovary is hard to see, for it obviously does tell the story when the force of connation has resulted in gamosepaly, gamopetaly and syncarpy; likewise when adnation has produced unions of stamens with petals or sepals, or amalgamated androecium, corolla, calyx and sometimes involucre, into a floral tube. A logical sequence would be the joining of the floral tube to the gynoecium, and vascular anatomy shows that in many cases this has taken place. The intermediate stages are there for us to see. If the union is a loose one, as in *Cichorium* or *Hedera helix*, the bundles in the inferior ovary wall are separate, but when adnation is extreme, bundles lying in the

same radii, and even adjacent ones, are fused into common cords, as in *Cordyline* and *Ananas*.

Eames and MacDaniels (1947), in their very lucid presentation of the flower (Chap. XIII), have called attention to some seemingly anomalous cases of inflorescence position which internal evidence shows have resulted from phylogenetic adnation. In *Streptopus* and *Sparganium* the inflorescence is located below, not above, the leaf, the usual position. Cross sections of the stems of these genera contain two steles, which makes it clear that the peduncle of each has fused with its axis and that the inflorescence belongs to the node below. In *Tilia*, on the other hand, where fusion between peduncle and bract is evident externally, only one stele is present, this the result of extreme concrescence. The two large families Rosaceae and Ericaceae are especially rich in series that demonstrate progressive stages in adnation of floral members. Although these have been discussed previously (1944), the evidence of phylogenetic adnations which they reveal deserves another examination.

Puri (1951, 1952a), in his criticism of MacDaniel's conclusions (1940) regarding the nature of the ovary wall in the apple, berated MacDaniels because of his reliance on the "out-of-date" van Tieghem principle, but he passed lightly over the clear evidence of progressive adnation present in the Rosaceae which MacDaniels had assembled from his own studies and those of Bonne (1928) and Jackson (1934). One character common to the members of this very variable family is the presence of a floral tube, which in the less advanced genera consists of a flattened disk. *Rubus* is a primitive genus, and in its disk the petal-stamen and sepal bundles are free from each other. *Fragaria* has taken a forward step by uniting the petal-stamen and sepal strands which lie in the same radii. In *Physocarpus* the disk has become a tube which is free from the gynoecium, but in *Spiraea* the tube has been contracted and united at its base to a syncarpous ovary. Fusion of the floral tube with the gynoecium has progressed toward the top of the ovary in *Amelanchier, Pyrus, Sorbus* and *Cydonia*. The levels at which the petal-stamen bundles separate from the common cords at the tube vary, the locus being lowest in the quince, higher in the apple, and highest in the pear, indicating corresponding degrees of advancement. *Agrimonia* is

particularly enlightening because its floral tube surrounds the carpels, but is not united with them. Similar tubes are not unknown in other families containing perigynous flowers. Buchet (1928), in a reply to Bugnon, called attention to pairs of closely related species in which the venation patterns are identical, but in one of which the foliar members are free, and in the other concrete with the ovary wall. They are, respectively: *Sorbus Aucuparia* and *S. hybrida, Alchemilla vulgaris* and *A. conjuncta* or *A. alpina, Chlora imperfoliata* and *C. perfoliata,* and *Endymion nutans* and *Hyacinthium.* Since the terminus of the receptacle can be located with reasonable accuracy at the insertion of the free floral tube in the perigynous species, it would seem logical to locate it in a corresponding position in the epigynous ones. After a careful study of the evidence supplied by rosaceous genera, it is difficult to interpret the ovary of the pome fruit in any way other than as MacDaniels has done. Floral diagrams of these genera may be found in MacDaniels' Figs. 4–10 of his 1940 memoir.

In concluding his latest article, Puri (1952a) suggests that, although little help can be obtained from anatomy in solving the problem of the inferior ovary, there are new approaches which will yield more reliable evidence; among them, detailed histogenetic and cytological studies. It is interesting to note that some recent cytological work on apple leaves, flowers and fruits does confirm the conclusion of MacDaniels. Working with 2x–4x periclinal chimeras of the Giant Rome variety, Blaser and Einset (1948, 1950) noted that strands of tetraploid cells, surrounded by diploid tissue, conformed in general to the vein system of both leaf and flower. Although the floral base of a young flower appears to be a simple ring, several growth zones are probably present, since closer examination reveals that the ring consists of several cycles of tetraploid cells separated by diploid ones. This pattern led the authors to conclude that in the apple flower "zonal growth is secondary to fusion". Although these fusions of floral whorls do not take place ontogenetically, they are reflected in the zonation patterns. Dermen (1953), also, working with 2x–2x–4x chimeras of the Winesap variety, concluded that the location of tetraploid tissue in floral members resembles that in

leaves, and for that reason the flesh of the apple fruit could be considered to be appendicular. Phylogenetically the apple flower and fruit seemed to him to represent compound structures.

Leinfellner (1954), however, whose ontogenetical studies have led him to believe that all inferior ovaries are contained in axial cups, has recently offered new evidence in support of his opinion. He made a comparison of the venation patterns of foliage leaves, bracts and sepals of *Rosa, Cydonia* and *Rhodotypus* of the Rosaceae, as well as of *Manetta and Philadelphus*. Even though all of these structures have undergone great condensation in their phylogeny, the course taken by the veins indicated to him that in each plant studied the appendages are homologous. Remnants of all parts of the leaf, including stipules, persisted within them. In consequence, since the veins of the sepals, which arose at the top of the hypanthium, followed a course similar to that of the leaves and he could find no evidence of sepal bases in the hypanthium, he concluded that the calyx was originating in stem tissue. The answer to this reasoning by a floral morphologist would be that one would not expect to find any evidence of separate sepal bases here, if congenital concrescence had reached an advanced stage, since the calyx bundles would have been indelibly fused with those of the adjacent whorls.

Schaeppi and Steindl (1950), also, as the result of a comparative ontogenetic study of the Rosoideae, concluded that the subfamily is a natural one and that an axial cup is present in all genera, although it can take different forms. In the tribe Potentilleae it is broad and flattened into a disk that is cone-shaped in the center and bears the calyx, corolla and androecium on its outward-curving edge. In the Kerrieae, the center is flat; in the Sanguisorbeae, depressed, with the sepals, petals and stamens arising from its under surface. The carpels which are borne in the depression are stalked and peltate. Vascular anatomy was not taken into account. They indorsed a general opinion that the disk is axial because petals, and sometimes sepals, are deciduous from it—but this is not inimical to the interpretation that the disk is appendicular, for we know that specialized leaves may have articulations from abscission layers at almost any point.

In one tribe of the Rosaceae, the Roseae, on the other hand, internal evidence shows that the hypanthium is truly axial. Here

one can find examples which suggest how an inferior ovary could have been produced, phylogenetically of course, by an invagination of the receptacle. G. H. Smith's work on *Calycanthus* (1928) and Jackson's on *Rosa* (1934) are well known. In flowers of these genera, in which the floral apex is concave, receptacular bundles ascend part way up in the wall of the cup, then turn downward, with phloem and xylem inverted, and in passing down give off branches to the carpels. It should be pointed out, however, that in these forms we are dealing with perigynous cups in which the carpels are free. In a true inferior ovary the union between the wall and gynoecium is complete. *Rosa* and *Calycanthus*, however, do show first stages in the production of an inferior ovary, such as is present in the Santalaceae. The terms " sinking ", " inpushing " and " invagination ", when used in connection with the floral axis, have been criticized by Puri who insisted that they " are just descriptive terms, which are used to describe the peculiar type of differential growth characteristic of certain floral axes ". He assumed that Smith and Smith (1942a, b) " want us to believe " that an actual inversion of the axis has occurred. These authors, however, did not intend that, and used the terms to describe the evolutionary process which took place in phylogeny, not what is occurring in ontogeny. From a personal communication of Frank H. Smith, the following is quoted: " Certainly the principles of phylogenetic fusion by differential growth are well established—at least I thought so. The idea never occurred to me that statements regarding invagination of the floral axis would be interpreted in any other way ".

The Ericaceae, also, is a family of especial value in revealing footprints on the sands of time, for it contains a series of flowers in whose ovarian structures one may find a whole range of variation from hypogyny through perigyny to epigyny. Among the hypogynous forms upon which Copeland (1943, 1947) and Palser (1951, 1954) worked, are many that contain the beginnings of adnation; this is manifest by the fusions of vascular bundles. Copeland's excellent diagrams of three-dimensional models greatly facilitate recognition of differences in the amounts of adnation which have taken place and the structures involved. These variations are of some taxonomic value, particularly in the delimitation of tribes. Palser (1951), in her study of 20 species of Androm-

edae, found only one, *Oxydendron arboreum,* in which all floral traces are independent. In all others the contiguous bundles of two or more whorls tended to unite. Anatomical differences resulting from various kinds and amounts of bundle fusions proved to be of some specific value, and certain patterns of relationship emerged from them.

The excellent series of diagrams of ericaceous flowers in the paper of Eames (1931), reproduced with new numbering from the writer's previous review (1944), illustrate well how originally separate floral whorls have been brought together in adnation and their bundles progressively fused (Figs. 25–30). In the hypogynous *Pyrola secunda* (Fig. 25), lack of adnation is reflected in the separation of bundles of each whorl. In *Andromeda glaucophylla* (Fig. 26) the stamen bases are adnate to the petals, and their respective traces are fused at the base. In *Gaylussacia frondosa* (Fig. 27) a floral tube, consisting of calyx, corolla and androecium elements, has become united with the ovary wall, but the vascular bundles are largely free. In the three species of *Vaccinium* (Figs. 28, 29, 30), however, progressively greater amounts of adnation of the stamen-petal strands with those of the dorsal carpel bundles have taken place. This series of forms, demonstrating progressive adnation, is so perfect that it is difficult, indeed, to doubt the appendicular nature of the inferior ovary here or to question the value of vascular anatomy in revealing the adnations which have taken place in phylogeny. Eames (1953) has found it of value in confirming the correctness of the recent transfer of the old genus *Chiogenes* to *Gaultheria.* The floral tube of *G.* (*Chiogenes*) *hispidula* becomes adnate to the ovary during the progress of flower to fruit, whereas in *G. procumbens* it grows up around the ovary but does not coalesce with it. Both species, however, are similar in their vascular anatomy and owe most of the bulk of their fruits to fleshy floral tubes. Chou (1952) studied two Pacific species of *Gaultheria, G. ovalifolia* and *G. shallon.* In flowers of these plants, postgenital fusions unite fleshy calyx segments, but the tube remains free from the ovary, as in *G. procumbens.*

It was suggested earlier in this paper that processes which have taken place during the phylogeny of some flowers are sometimes duplicated in their ontogeny. This is especially true of unions

which take place in and between the carpels. These postgenital fusions have been given new emphasis by Baum and Leinfellner. Baum (1948a, b) studied the fusions which unite the carpel edges and the carpel sides. In certain syncarpous ovaries in which the carpels are congenitally fused at the base, postgenital fusions continue the sealing processes above. If these fail to reach the summit, the upper part of the ovary remains paracarpous. The degree of concrescence varies from a loose one, in which epidermal cells are clearly visible, to a fusion so extreme that there is no trace of the carpel edges. Sometimes interlocking papillae may be found in the septal spaces (Baum, 1950). Both Baum and Leinfellner (1951) were impressed by the similarity of the histological patterns resulting from congenital and postgenital fusions in some of their flowers. Others have noted ontogenetical unions which appeared to be extensions of phylogenetic ones. They include Abbas (1952), in two tribes of the Liliaceae; Boke (1948), in *Vinca rosea;* Satina and Blakeslee (1943) and Satina (1944), in *Datura;* Miller and Wetmore (1945), in *Phlox Drummondii;* Morf (1950), in *Saxifraga;* Tepfer (1953), in *Aquilegia.* It is logical to infer that ontogenetic unions that took place in ancestral flowers are made apparent by congenital fusions. In *Gaultheria hispidula,* as has been noted, the floral tube becomes united with the ovary by a post-genital fusion, and in *Annamocarya* the ovary is joined to the husk by the growth of an intercalary meristem.

Boke (1948) reported a very interesting phenomenon in the development of the corolla tube of *Vinca rosea.* Its lower part, to which the stamens are attached, arises by zonal growth, whereas the segments of its upper part become connate through ontogenetic fusion. He was inclined to think that the basal segment of the tube was receptacular because stomata, very abundant on the upper section, were absent from the lower region except near the insertion of the stamens. Since the presence of stomata is characteristic of stems as well as of leaves, there is no need for Boke to discard the view that the lower part of the tube is also floral. It can better be regarded as a region where zonal growth is taking place in congenitally united stamen and petal bases. It would be surprising if the receptacle were to bulge upward into a tube surrounding the ovary and not carry the calyx. In Boke's excellent

photographs (his Figs. 19–23) the tissue of the lower part of the floral tube has a different aspect from that of the receptacle below, and the beginning of the tube is well marked.

DESCRIPTIVE TERMS

Because many of the terms now used in the descriptions of the inferior ovary are "(1) misleading or incorrect in etymology, (2) do not permit a reasonable classification into mutually exclusive types, and/or (3) differ in interpretation by different botanists", Egler (1951) has suggested a revised set of terms, the adoption of which would make the task of describing ovaries simpler for the teacher as well as the taxonomist. He separates them into six types, in which two factors that he designated as "abovarian" (away from) and "adovarian" (adnate to) are present in combination of three degrees of freedom of an "androperianth" (floral tube) from the ovary. Since the term "floral tube" has been used in different ways, he substituted "androperianth". The latter may consist of a "casing", enveloping the ovary; of a "collar", which surrounds but does not touch it; or of both a "casing" and a "collar". Of the adovarian series: in his type I (lily type) all parts are free; in type II (witch hazel type) the androperianth consists of casing only, which is half-adnate to the ovary, while the structures above are free; in type III (carrot type) the androperianth consists of a casing only which is fully adnate. Of the abovarian series: in type IV (cherry type) the androperianth consists of a collar only; in type V (Aronia type) of a half-adnate casing, surmounted by a collar; and in type VI (apple type) of a casing, which is fully adnate, surmounted by a collar. The present writer certainly regrets that she was born too soon to have made use of these terms in her teaching.

That Parkin (1955), on whom we have always been able to count to bring us back to earth when our imaginative flights have been too fanciful, would approve of the addition of more terms to the over-burdened gynoecium, is doubtful. He has made another "stocktaking", and this time is asking for a simplification of the terminology. To begin with, he sees no sense in the use of four different spellings of the term. "Gynoecium" seems to be the correct one. He would discard "pistil" and "pistillate" as unneces-

sary, but retain "carpel" and "carpellate". "Receptacle" is a better term than "thalamus" or "torus". "Polymorphism", in the sense in which Saunders used it, should go; and, as far as "phyllospory" and "stachyospory" are concerned, Eames "has well nigh brought Lam's contention to a *reductio ad absurdum*". Parkin no longer ascribes importance to the so-called terminal carpel or terminal ovule, since it has been proven to his satisfaction that this position is a derived one. "Troll's somewhat revolutionary classification of placentae" seems to have made so "little impression on botanists generally (and perhaps some of us are glad that it appears to be so!)" that the terms "coenocarpy" and "paracarpy" are superfluous, and "peltate" and "epeltate" carpels of minor importance. The terms "marginal", parietal", "axile" or "falsely axile", "free central" and "laminar" take care of the placentation. He is in favor of adopting the term "stylode" for the "style" of a single carpel, keeping the latter term for the compound structure of a syncarpous gynoecium. All inferior ovaries appear to him to be phylogenetically of adnation origin, and whether or not the receptacle is involved is of minor importance, since invagination is to be explained by complications arising through intercalary meristems. The term "hypanthium", therefore, should be discarded in favor of "floral tube".

CONCLUSIONS

The description by the psychologist, Boring (1954), of the way in which science progresses is enlightening but not very flattering to us scientists who pride ourselves on being objective. He noted two factors which are always operating to a greater or lesser degree in the drawing up of scientific theories. These are the "ego-involvement" and the "climate of opinion" (Goethe's "Zeitgeist"). Regarding the former, he says: "You do not have to go very far toward neurosis, however, to find the personal equation making trouble in science. You have to go only far enough to find egoism, which would seem to be no distance at all". A certain amount of egoism, he admits, is necessary, otherwise there would be no motivation, no drive or enthusiasm. Carried to extremes, however, it creates bitter controversy. The second factor, the "Zeitgeist", appears to Boring to be more subtle in its work-

ing. Consciously or subconsciously, one is influenced by conventional thought and unquestioned assumptions that are implicit in the culture in general or science in particular. They may act as "vires inertiae" to constrain originality and reinforce tradition, and progress is held back. They are not without salutary effects, however, in spite of the slowing down of progress, for they make for caution and judiciousness, and serve to restrain cranks. Boring's conclusion is that, although the acceptance of scientific truth is delayed, it does come about in the end, sometimes after a generation or more. If one wished to find specific instances to illustrate Boring's thesis, one could find no better place in which to look than in the history of floral anatomy during the last 200 years, especially in that phase of it which concerns the inferior ovary.

SUMMARY

Within the last 12 years knowledge concerning the inferior ovary has been extended, but controversy has not terminated. As the result of anatomical studies, appendicular inferior ovaries have been reported in various genera of the following families: Agavaceae, Araliaceae, Begoniaceae, Bromeliaceae, Caprifoliaceae, Celastraceae, Compositae, Cornaceae, Ericaceae, Orchidaceae and Rubiaceae, and in *Juglans* of the Juglandaceae. The receptacular cup type, with ascending and recurrent budles in the wall, present in *Darbya* seems to be characteristic of the Santalaceae as a whole, of the Loranthaceae, of *Carya* and *Annamocarya* of the Juglandaceae, and of the Cactaceae. True inferior ovaries, in which the outer structures are fused with the ovary, should be distinguished from perigynous cups, as are found in *Rosa* and *Calycanthus*. Recently the value of using the anatomical method in solving the problem of the structure of the inferior ovary has been questioned because of facts which have come out of modern studies in histogenesis and morphogenesis. It should be emphasized, however, that these facts are concerned with ontogeny. Plant morphologists have found that vascular anatomy, when used in comparative studies, has been a most valuable tool in the reconstruction of plant phylogenies, and they see no valid reason why it is not conclusive in the determination of the nature of the inferior ovary wall.

ACKNOWLEDGMENTS

In conclusion the writer wishes to express her very great appreciation to the many who have aided in the preparation of this paper. Especially helpful were Dr. A. J. Eames, who made many suggestions and read the greater part of the manuscript; Miss Marjorie W. Stone, who located some of the literature difficult to find; to Dr. V. Puri, for permission to use his figures Nos. 1–3; and to Dr. Su-ying Liu, for inking the diagrams. Thanks are also due to Dr. Reed C. Rollins for his kindness in allowing her the use of the books in the Gray Herbarium Library.

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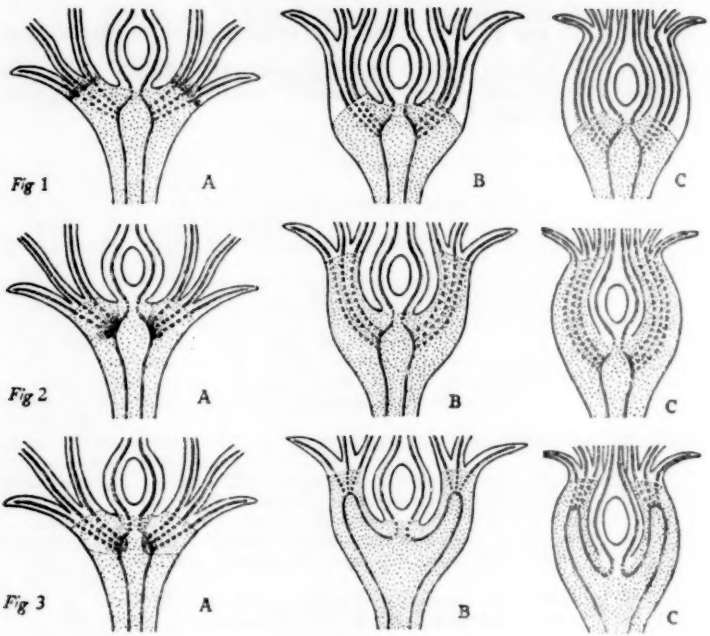


PLATE 1

FIGS. 1–3 (after Puri). Schematic representation of the three possible ways in which an inferior ovary can originate. The dotted regions represent the receptacle while the more densely dotted areas in A indicate the centers of most active growth; broken lines represent the "trace" parts of vascular bundles and dotted lines the phloem.

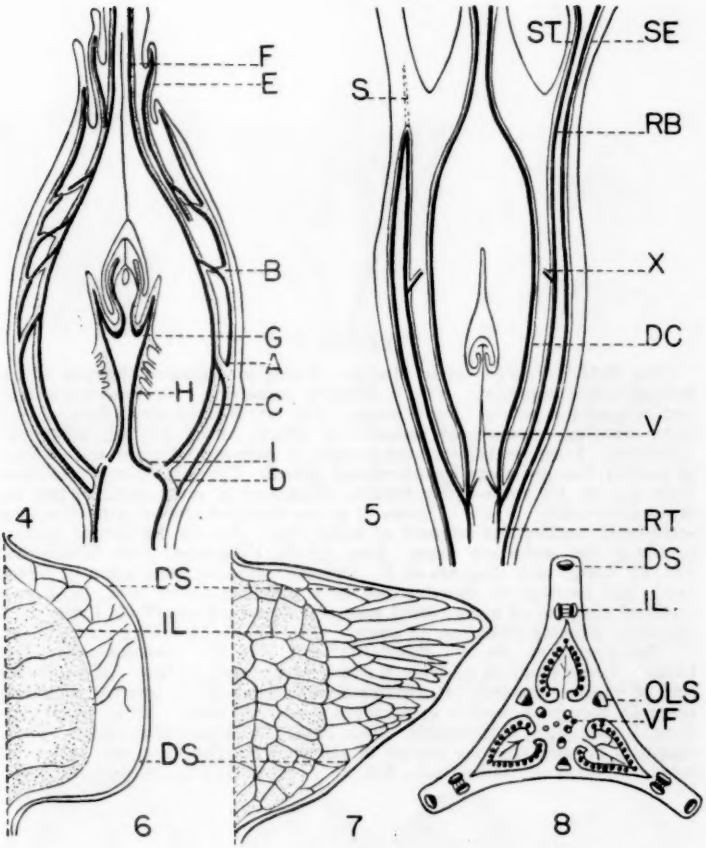
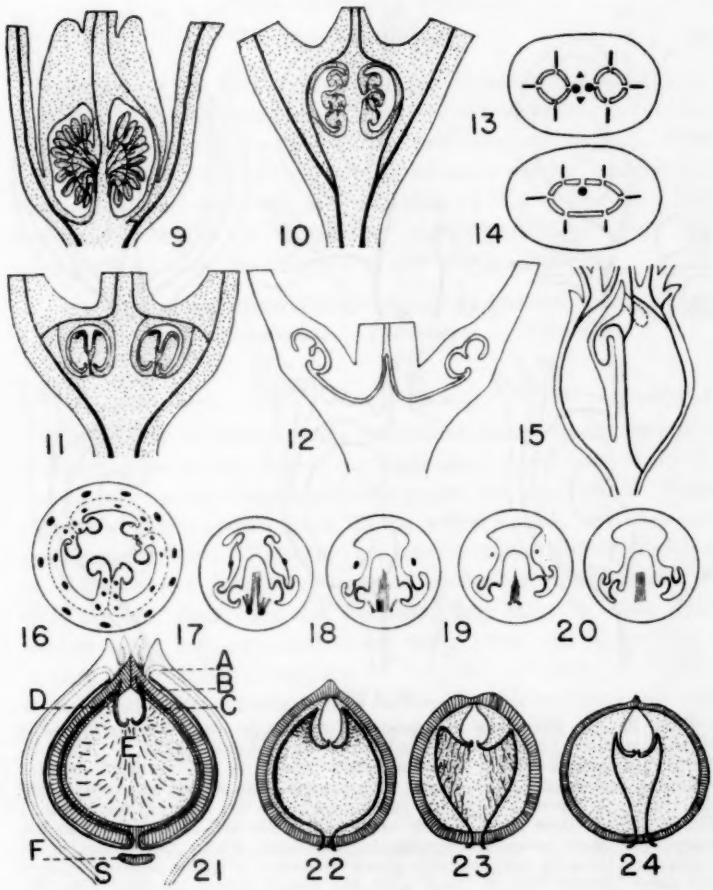


PLATE 2

FIG. 4. *Juglans regia*—after Nast. Diagram of a flower cut through the major septum. Xylem is indicated in black; phloem is stippled. A, normally oriented branch from involucre to perianth-carpel cycle; B, twisted branch; C, perianth-carpel cycle; D, perianth-carpel bundle from pedicel; E, perianth bundle; F, bundle of style; G, ovule trace; H, ventral bundle; I, accessory branches joining the ventral bundles. FIG. 5, *Darbya*—after Smith and Smith. Reconstructed long. diagram through two dorsal traces, a sepal and stamen on one side and between sepals on the other. SE, sepal trace; ST, stamen trace; DC, dorsal carpellary trace; S, sclerenchyma; RB, recurrent bundle; RT, residual tissue; X, branch traces. FIGS. 6–8, *Begonia*—after Gauthier. FIG. 6, *B. socotrana*, dia. long. sect.; FIG. 7, *B. octopetala*, dia. long. section; FIG. 8, *B. socotrana*, dia. cross. sect.; DS, dorsal-sepal-dorsal-carpel trace; IL, inner lateral trace; OLS, compound bundle of the flat side; VF, ventrals.

PLATE 3

FIGS. 9–12. *Mouriri*—after Morley. Series of diagrams showing vascularization and reduction. FIG. 9, *Miconia guianensis*. Reconstructed long. sect., showing a nearly "free" ovary. FIG. 10, *Mouriri trunciflora*. Long. sect., showing adnation of perianth to ovary. FIGS. 11, 12, sub-genus, *Pericrene*. Long. sects., showing results of extreme adnation and shifting of position brought about by differential growth. FIG. 12, *Mouriri cauliflora*. FIGS. 13, 14, *Mitchella*—after Blaser. Diagrams of cross sects. of two inflorescence steles. FIG. 13, Steles of a two-flowered cluster with diverging sepal-petal bundles and remnant of axial stele. FIG. 14, Section of an axis in which two steles are fused. FIGS. 15–20, *Viburnum*—after Wilkinson: FIG. 15, Long. sect. diagram of *V. Sieboldii*, showing attachment of fertile ovule and location of abortive one in a different plane; FIG. 16, Cross-sectional diagram of a postulated ancestral flower; FIGS. 17–20, Cross. sect. diagrams showing reduction of ovules; FIG. 17, *V. Sieboldii*; FIGS. 18, 19, *V. Lentago*; FIG. 20, *V. rhitidophyllum*; FIG. 21, *Annamocarya*—after Leroy. Long. diagram of fruit in plane of primary septum. A, ascending ring of bundles in cupule; B, recurrent ring in cupule; C, internal ascending ring; D, recurrent bundles in partition bordering locule; E, septal irradiations; F, plexus; S, stelar bundle. FIGS. 22, 23, 24, *Carya*—after Leroy. Long. diagrams of nuts, showing retreat of placental bundles from wall to central column; FIG. 22, *C. cathayensis*; FIG. 23, *C. Polanei*; FIG. 24, *C. cordiformis*.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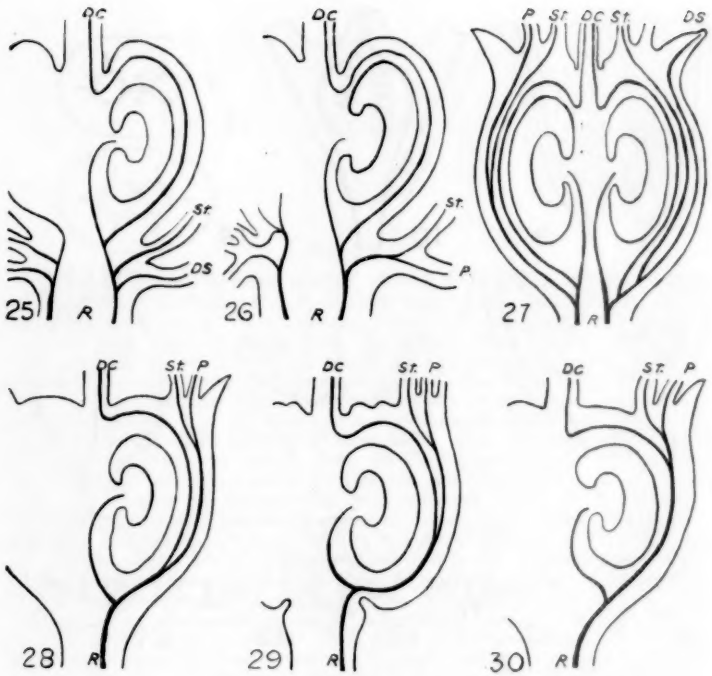

PLATE 4

FIGS. 25–30. Diagrams of ericaceous flowers to show stages in fusion of the vascular skeleton under adnation—after Eames (1931). FIG. 25. *Pyrola secunda*, a typical superior ovary type with no fusion of organs; FIG. 26, *Andromeda glaucophyla*, with stamen base adnate to corolla, and the traces of these two organs fused nearly to the base of the stamen; FIG. 27, *Gaylussacia frondosa*, the stamens, corolla and calyx adnate to the ovary, but their vascular supplies largely free; FIGS. 28–30, species of *Vaccinium*, showing progressively greater amounts of fusion between stamen and petal bundles and of these with the dorsal carpel bundles: FIG. 28, *V. vacillans*; FIG. 29, *V. pensylvanicum*; FIG. 30, *V. macrocarpon*. FT, DS, St., P, DC, VC, R indicate respectively floral tube, and the dorsal-sepal, stamen, petal, dorsal-carpel, ventral-carpel and stelar bundles.

THE OEDOGONIACEAE. III [1]

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Research on the Oedogoniaceae in the decade just past has considerably increased over that of either of the ten-year periods immediately preceding the dates of the two previous reviews. Part of this may be due to the resumption of more normal programs of research all over the world after the close of World War II. It is evidenced both by the increase of papers published (over 100 since 1946) and in the numbers of new species described.

NUMBER OF SPECIES RECOGNIZED IN THE OEDOGONIACEAE

	Oedogonium	*Bulbochaete*	*Oedocladium*
1936	296	66	6
1946	322	67	9
1956	380	89	10

It is difficult to make a really exhaustive survey of the literature involved, even limited to this one algal family, and there is always the probability that some important papers are overlooked. Many reprints of algal papers come to the writer's desk, and they are greatly appreciated. New taxa are usually quite faithfully indexed in abstracts and reviews of various kinds, but investigations of algal ecology, physiology and chemistry may occur in many journals of many languages and under many titles. An abstract or a review may mention analyses of "algae" or even of "green algae", but either category takes in considerable territory and may or may not refer to the Oedogoniaceae. Even the titles of some papers leave much to be desired. The writer once found a choice nugget about the Oedogoniaceae in a paper titled ". . . in unicellular algae". In spite of this find, the writer has consistently refused to examine articles whose titles implied they were not concerned with the Oedogoniaceae. One simply must acknowledge that his best can not be complete; *nec reperire fas est omnia.*

The review that follows is divided into several sections, not necessarily mutually exclusive, but affording topics around which data may be assembled.

[1] Supplement to articles in The Botanical Review **2**: 456–473. 1936; **12**: 530–534. 1946.

MORPHOLOGY AND TAXONOMY

The Oedogoniaceae, comprising the genera *Oedogonium*, *Bulbochaete* and *Oedocladium*, constitutes the single family of the order Oedogoniales, class Chlorophyceae, and phylum Chlorophyta. No data have appeared that would indicate any change in the usual taxonomic position of the group among the algae. Papenfuss (64) has proposed that the phylum name "Chlorophyta" be replaced by "Chlorophycophyta". General discussions of the Oedogoniaceae during the past decade include those of Smith (92) and Lacerda (50). Briefer accounts of the characteristics and classification of the family are found in Prescott (74), Tiffany and Britton (104), Bock and Bock (6), Melchior and Wedermann (58), Papenfuss (66) and Forest (30).

In the genus *Bulbochaete* new species have been described by Bock and Bock (6) from Germany (*B. pseudoareolata, B. pseudoscrobiculata, B. punctocostata, B. verrucosa*); by Gauthier-Lievre (34) from Africa (*B. congolensis, B. nigerica, B. trochainii*); by Skuja (91) from Burma (*B. burmensis, B. kosmoceps*); by Hughes (40) from Nova Scotia, Canada (*B. citriformis, B. granulata, B. wailesii*); by Prescott, Silva and Wade (77) from the Gaspé Peninsula, Canada (*B. glabra*); by Jao (42, 43) from China (*B. triangularis, B. sphaerocarpa, B. pseudoelatior*); by Ley (53) from China (*B. macrandria*); by Singh (90) from India (*B. bharadwajai*); by Lacerda (50) from Portugal (*B. palhinhae, B. resendeana, B. tiffanii, B. echinospora*) —22 new species.

In the genus *Oedogonium* the new species are described by Andersen (2) for Denmark (*Oe. amagarense* Hallas, *Oe. citriforme* Hallas, *Oe. incrassum* Hallas, *Oe. praelongum* Hallas, *Oe. rosenvingii* Hallas, *Oe. transversum* Hallas); by Bock and Bock (6) for Germany (*Oe. franconium, Oe. spiralicostatum*); by Britton (12) for the Philippine Islands (*Oe. circumlineatum, Oe. paloense, Oe. philippinense, Oe. visayense*); by Cholnoky (18) for Mozambique (*Oe. schweickerdtii*); by Hughes (40) for Nova Scotia, Canada (*Oe. regium*); by Jao (42, 43) for China (*Oe. cylindricum, Oe. excentriporum, Oe. subspiralidens, Oe. kwangsiense, Oe. nitidum, Oe. pseudaureum*); by Ley (53) for south China (*Oe. cantonense, Oe. exile, Oe. kwantungense, Oe. speciosum, Oe. subplagiostomum*); by Lacerda (49, 50, 51) for Portu-

gal (*Oe. broterianum, Oe. figueirense, Oe. carrisoi, Oe. echinospirale, Oe. leiriense, Oe. henriquesii, Oe. allorgeanum, Oe. nigrum, Oe. aveirense, Oe. lusitanicum, Oe. quintanilhae, Oe. granulosporum, Oe. esterrejae, Oe. lisbonense, Oe. lopesianum, Oe. taftii*;[2] by Silva (88) for Tennessee, U.S.A. (*Oe. sphaericoinconspicuum*); by Tiffany (100) for New Zealand (*Oe. chapmanii*); by Tiffany (102) for the Philippine Islands (*Oe. discretum, Oe. pudicum*); by Tiffany (101) for Saaremaa Island in the Baltic [*Oe. stictospermum* (Skuja)]; by Villeret (110) for France (*Oe. armoricanum, Oe. bourrellyanum, Oe. delacerdanum, Oe. erceense*); by Singh (90) for India (*Oe. gorakhporense, Oe. mesospirale, Oe. ellipsosporum, Oe. mesodentatum, Oe. kushmiense*); by Skuja (91) for Burma (*Oe. acrospirum, Oe. khannae, Oe. episthostomum*)—58 new species.

A new species of *Oedocladium* (*O. tiffanyanum*) is described by Cribb (19) for Queensland, Australia. This is the tenth completely described species of the genus and the first one reported from Australia. It is the only dioecious-macrandrous species in the genus, and thus all the types of sexual reproduction known for the genera *Bulbochaete* and *Oedogonium* are now reported for *Oedocladium*.

According to the current Code, the nomenclature of the Oedogoniaceae starts with Hirn (38), and *Oedogonium* has been designated a *nomen conservandum*. Doty (24), expressing the viewpoint that a conserved name is not necessarily conserved against all other names for all time, feels that in some respects "Chantransia" might be the legitimate name instead of "Oedogonium". Papenfuss (65) has examined the status of "Chantransia" and designates it as a synonym of the already conserved "Oedogonium". Silva (89), on the other hand, thinks that "Oedogonium" is incorrectly conserved as over against "Prolifera". It is to be doubted that phycologists in general will consent to the removal of such a well-known epithet as "Oedogonium" from the conserved algal genera, nor would it appear to improve algal taxonomy to do so.

Much has been made in differentiating among species, particularly in the genera *Bulbochaete* and *Oedogonium*, of such charac-

[2] Since the specific name *taftii* has been preempted in the genus (see Tiffany, 98), this taxon may be designated *Oe.* **mirae** nom. nov.

teristics as shape of oogonia and of spores, ornamentation of spore walls, and cell dimensions, superimposed on the usually very definite differences based on sexual expression. In some species the value of such structural features is hard to assess, and separation of these species from others is sometimes difficult. Bock and Bock (6) discuss the variations encountered in such species in some detail but offer no substitute characteristics to be used or no plan for the reevaluation of such difficult taxa. These same authors (6) report the preponderance of female over male filaments in the dioecious species having no dwarf males. This may be more apparent than real because male filaments break up at the time of liberation of sperms from the antheridia.

There has been some discussion among phycologists as to the value of the provisions of the current Code, now making it mandatory to have a description in Latin if a new species or other taxon is to be recognized as having been validly described. Oedogoniologists have in general followed the provisions of the Code in this respect. Lund (54) has suggested that diagnoses of algae be given in two languages, one of which shall be French, German or English; and that, moreover, adequate illustrations along with complete dimensions be supplied.

Drew (25), in a review of algal life histories, uses *Oedogonium capillare* Kütz. to exemplify the freshwater monophasic type of algae having also certain extreme specializations.

ECOLOGY AND DISTRIBUTION

Since so many algal habitats in the world have not yet been adequately surveyed for specimens of this group, some facets of the distribution of the Oedogoniaceae can only be surmised. The fact that nearly all the species live in freshwater habitats (some are terrestrial and a few are brackish) reduces the complexities somewhat. It probably is true that many freshwater habitats the world over are at some times essentially similar, but, on the other hand, the microenvironments of even a single habitat may be quite dissimilar and thus support diverse algal populations. Some of these factors have been studied. Prescott (76) has assembled a very comprehensive list of papers dealing with algal ecology, and a few of the papers specifically refer to investigations on the Oedogoniaceae.

It is natural to assume that the species of the Oedogoniaceae are influenced in their growth, as are other filamentous algae and indeed plants in general, by differences in light, temperature, pH, and availability of necessary gases and mineral salts, but specific data are far from complete. Species of the aquatic Oedogoniaceae survive in a wide range of temperature, but reproductive structures rarely appear at water temperatures below 6 or above 32° C. Kleerekoper (47) found eight species of *Oedogonium* growing in temporary marshes with a pH limited to 6.2 to 6.6. Bock (5) identified 22 species of this genus in waters ranging from a pH of 6 to one of 9. Fruiting oedogonia have been identified from waters whose pH ranged from 3 to 9, but most species occur in habitats of near neutrality or somewhat alkaline.

Working with algae collected from the Aswan Reservoir (Egypt), Abdin (1) confirms an observation made many years ago by Transeau (106) that *Oedogonium* reaches its maximal development and reproduces in rather strong light. Some species can endure a great deal of shade, as is evidenced by their growth at considerable depths—greater, for example, than is true for *Stigeoclonium*. Most species of *Oedogonium* (and to a lesser extent *Bulbochaete*) are annuals with definite seasonal periodicities, although some persist vegetatively from year to year, as pointed out earlier by Transeau (106) and by Tiffany and Transeau (105) for the central states of the United States. Similar periodicities, differing in calendar dates but corresponding seasonally, appear to occur in all temperate zone areas, as noted by Bock (5) for Germany, Lacerda (50) for Portugal, and many data for continental North America. Bock and Bock (6) find two fruiting maxima for *Oedogonium* in Germany and France, one from late April to late June, the other (lesser) one in August, although some species fruit from late April to October. These authors (6) also report fruiting *Bulbochaete* from May to October, or occasionally later, with a single not clearly defined maximum from late July to the end of August.

Tiffany (103), in a survey of the data on geographical distribution of the Oedogoniaceae in North America, reports that some species of *Oedogonium* and *Bulbochaete* are cosmopolitan, a few are arctic, most occur in the temperate zone, many are both temperate and subtropical, and that the largest assembly of species

currently is in the Great Lakes region of the United States, with lesser extensions along the Mississippi valley and along the Atlantic coast from Nova Scotia to Florida and into the West Indies. He (103) makes the suggestion that perhaps the area south of the Great Lakes may have been a center of distribution for many species of *Bulbochaete* and *Oedogonium* that escaped the invasions of the seas and the Pleistocene glaciation. The arctic species may represent relicts of an earlier circumpolar distribution or hardy survivors of the vicissitudes of polar climates. The generally large species of *Oedogonium* in the tropics and subtropics may be polyploids, but this hypothesis has no confirmation at present.

The ten species of *Oedocladium* presents no discernible pattern of distribution, geographical or otherwise. All but one species (*O. hazenii* Lewis from New Jersey) are terrestrial and are usually found growing on the ground with *Vaucheria*, liverworts, protonemata of mosses, and sometimes the larger blue-green algae. The species reported from India grow at altitudes of 3,000 to 5,000 feet, but those in North America are found at much lower elevations. Cribb (19) reports a new species of *Oedocladium* from Queensland, Australia, having a habitat similar to those growing in the United States. Similarly the first described species of the genus (*O. protonema* Stahl) was reported from Germany, growing on the ground among pines. Incidentally this species has not been collected anywhere since its original discovery by Stahl (94).

In America one species of *Oedocladium* comes from Virginia, one from Massachusetts, one from New Jersey, one from North Carolina, and one from Florida. *Oedocladium operculatum* Tiffany, originally described from Puerto Rico and common in India, has been found by Whitford (112) in Mississippi. Vegetative filaments of unknown species of *Oedocladium* occur in Arkansas and in Virginia. Fruiting is apparently limited to spring and fall. It is likely that diligent search will reveal a fairly general distribution of *Oedocladium* in southeastern United States and on similar soils throughout the world. If not, the distribution of the genus must be considered as sparse, sporadic and without evident pattern, except for the fact that the plants apparently cannot vegetatively perennate through severe winters.

Species of *Oedogonium* and *Bulbochaete* have holdfast cells by

which they are anchored, sometimes only temporarily, to various substrates. Sometimes *Oedogonium*, in particular, forms large floating masses in ponds and lakes (Markle, 55), and occasionally parts of filaments appear as facultative planktonts (Ruttner, 84). Jørgensen (45) reports species of both genera as epiphytes on higher plants, and this is especially true of *Bulbochaete* and the smaller species of *Oedogonium*. Filaments may often be collected merely by scraping submerged stems or leaf sheaths of macrophytes or by microscopic examination of other filamentous algae, such as *Cladophora, Rhizoclonium, Vaucheria,* charophytes, or on other *Oedogonium* filaments. Skuja (91) finds young plants of *Oedogonium pusillum* Kirchner inhabiting the mucilaginous exterior of *Mougeotia* cells. Bock and Bock (6) report an "Oedogonium stage" of great abundance in some habitats in Germany with *Oe. upsaliense* Wittr., *Oe. autumnale* Wittr. and *Oe. inversum* Wittr. as the dominants, and six other species of the genus in lesser numbers.

Fritsch (32) notes the attachment of a new euglenid (*Colacium epiphyticum*) to vegetative filaments of both *Bulbochaete* and *Oedogonium*. Messikommer (59) finds that ducks use *Oedogonium* filaments for food, as evidenced by an examination of duck feces. Jones (44) reports both *Bulbochaete* and *Oedogonium* as food for the minnow (*Phoxinus phoxinus*) in the British Towy River. *Oedogonium* and *Bulbochaete* are likely to be found in most lakes and ponds (if not too deep) where a growing season is ample, and Gustafson (37) finds *Oedogonium* to be the commonest filamentous alga in the lakes of northern Massachusetts. Most filamentous algae may be removed, if noxious, by mechanical means or by application of dilute solutions of copper and arsenical compounds (Surber, 95). Commercial brands of algal removers are also available.

Species of neither *Bulbochaete* nor *Oedogonium* are common in running water, in spite of their holdfasts, and are rare on sandy bottoms of natural waters and of filter beds as well (Blum, 4; Brook, 14, 15; Kleerekoper, 47; Bock and Bock, 6). Jones (44), however, found *Oedogonium* abundant in the unpolluted Towy River of Britain with its stable pebble-gravel bottom and its soft, nearly neutral, waters.

Although the Oedogoniaceae are not represented in the ocean,

there is some indication that a few species may grow in brackish waters near the sea (Bourrelly, 8; Whitford, 113; Tiffany, 103). Croasdale (20) finds *Oedogonium idioandrosporum* (Nordst. and Wittr.) Tiffany on Penikese Island off the southern elbow of Cape Cod (U.S.A.) in a brackish pond having a salinity of 0.8.

Additions to our knowledge of the geographical distribution of the Oedogoniaceae in the last decade have been supplied by many workers distributed throughout the world. Besides those describing new species in the group, the following have contributed to the distribution of the already known species: Leake (52) for Oklahoma, McNeill (57) for West Virginia, Taft (96) for the Dakotas, Prescott (74) for the Great Lakes region, Forest (30) for southeastern United States, Wade (111) and Phinney (69) for Michigan, Tiffany and Britton (104) and Phinney (68) for Illinois, Thompson (97) for Kansas, Drouet (26) for Minnesota, Schumacher and Muenscher (85) for Washington, Whitford (112, 114) for Mississippi and North Carolina, and Nielsen and Madsen (63) for Florida—all from the United States; Hughes (40, 41) for Canada, Prescott (73) for Panama; Fritsch (32) for Great Britain, Bock and Bock (6) and Klotter (48) for Germany, Bourrelly (7, 8) and Villeret (110) for France, Bourrelly and Manguin (10, 11) for the Azores and for Guadeloupe, Messikommer (60, 61, 62) for Germany and Switzerland, Rosa (83) for Czechoslovakia, Jørgensen (45) for Denmark, and Woodhead and Tweed (115) for Great Britain—all from Europe; Behre (3) and Britton (12, 13) for the Philippine Islands; Kleerekoper (47) for Brazil; Cholnoky (18) and Gauthier-Lievre (33) for Africa; Jao (42, 43) and Ley (53) for China; Singh (90) and Gonzalves and Sonnad (35) for India; Rayss (81) for Palestine; Skuja (91) for Burma.

CYTOLOGY AND CELL BEHAVIOR

The prominent nucleus and chloroplasts, the relatively small number of chromosomes, and the cell size of many species make members of the Oedogoniaceae good subjects for cytological investigations. Bold (in Smith, 93) makes a comprehensive review of algal cytology with numerous references to the Oedogoniaceae. Schussnig (86) assesses the general features of mitosis in the genus *Oedogonium*. Dangeard (21) discusses some of the known

data about plastids, vacuoles, blepharoplasts, especially in *Oedogonium*, with brief notice of the plastids in *Bulbochaete*. Dangeard (22) reports the presence of grana in the chloroplasts of *Oedogonium*. Chadefaud (17) emphasizes the value of plastids, particularly peripheral plastids, in algal systematics. The unique method of cell division in the family results in the formation of the well-known "apical caps". The number of apical caps possessed by a cell may be one to many, especially in *Oedogonium*, and this number corresponds to the number of divisions the cell has undergone. Brunel (16) has noted 21 apical caps in a single cell of an unspecified species of *Oedogonium*, and this is probably a record. Tschermak (109) states that the behavior of chromosomes in *Oedogonium* parallels that in the seed plants, and that the volume of chromosomes is relatively smaller in species having smaller cells.

The effects of colchicine on nuclear and cell division have been reported for many plants, and some species of *Oedogonium* have been investigated in relation to this substance. Gorter (36) finds that application of dilute solutions of colchicine to *Oedogonium* filaments results in a swelling of newly formed cell walls and in the development of local thickenings on the walls; neither nuclear nor cell division takes place. Tschermak (107) in 1942 reported induction of polyploidy in various species of *Oedogonium* by immersing the plants in a 1% solution of colchicine in from five to eight hours. Polyploidy occurred only when cells were in metaphase; suppression of cells took place at prophase and malformations at telophase stages. Eigsti and Dustin (27), in their comprehensive survey of the effects of colchicine on various organisms, express doubt of Tschermak's results because of the inadequacy of cytological evidence. Tschermak (108, 109) in later papers further states that diploid filaments of *Oedogonium* can be produced from normal haploid plants by application of colchicine, and that the diploid plants are characterized by having double the surface area of cells and two to three times the volume, larger chromatophores and usually more numerous pyrenoids as compared to the haploids. Tschermak (108) also finds diploid species of *Oedogonium* in nature and states that natural polyploids and those artificially produced have essentially the same characteristic features.

The numbers of chromosomes in the cells of Oedogonium spe-

cies have been reported from time to time, and recent reports are those of Lacerda (50) and Tschermak (109). In *Oe. cyathigerum* Wittr. n = 19, in *Oe. grande* Wittr. n = 13, and in *Oe. pachyandrium* Wittr. n = 15 [or (?) 17]. Additional reports not indicating the species may be summarized:

n = 9 in 3 species
13 in 6 species
17 in 5 species
18 in 2 species
19 in 3 species

The rather extensive list of chromosome numbers in cryptogamic species of plants in the tractate by Delay (23) unfortunately does not include members of the Oedogoniaceae.

Ever since Nathan Pringsheim (79) in 1858 noted sexuality in *Oedogonium*, the migration of the sperm to and into the oogonium and its subsequent union with the egg have intrigued phycologists who have wondered at the mechanisms involved. It is equally fascinating to observe the behavior of the androspore in the nannandrous species as it escapes from the androsporangium, swims to the oogonium or very near it, settles on the oogonium (but never enters it) or on adjacent cells, and germinates into a very small filament capable of producing antheridia and sperms. This story has been recorded only a few times. Erady (28) has a paper ready for the press describing and figuring many of the events from the germination of the androspore and growth and sperm production of a unicellular dwarf male in a new species of *Oedogonium*—the successive series of development from the escape of the androspore from the androsporangium to the formation and escape of the sperms from the dwarf male.

Although the androspore almost always germinates on the oogonium or an adjacent cell, the writer has noted in a few instances that germination may occur on a cell of some other alga, such as that of *Cladophora*, if that cell is in juxtaposition with the oogonial cell. The behavior of both the sperm and the androspore suggests the formation of chemical substances (hormones), at least by the female cells, to which these flagellated cells respond. The zoospores, on the other hand, will germinate on almost any substrate and apparently are not influenced by secretions from the

sexual cells. In view of the classic investigations of Raper (80) on *Achlya* (a fungus) and other research on sexual aspects of algae and fungi, similar formations of sex hormones in the Oedogoniaceae seem probable. It is hoped that the techniques necessary to analyze the sexual behavior of sperms and androspores in the Oedogoniaceae, admittedly difficult, may be solved at an early date.

PHYSIOLOGICAL AND CHEMICAL REACTIONS

Fogg (29) gives an excellent summary of algal metabolism in general, but little space is devoted to the Oedogoniaceae. There appear to be no consistent differences between the fatty acids in the different classes of algae and those in the higher plants of similar habitats. Fogg (29) records that unsaturated fatty acids, especially those with 16, 18 and 20 carbons, predominate in *Oedogonium*. Palmitic acid is the most abundant of the saturated fatty acids. The unsaponifiable lipoid fractions of all algae perhaps have small amounts of the hydrocarbon hentriacontane ($C_{31}H_{64}$). Apparently only one of the sterols (sistosterol) is to be found in *Oedogonium*.

Höfler and Schindler (39) and Kinzel (46) discuss reactions of cell walls and some epiphytes of *Oedogonium* to vital stains. Prát (70, 71, 72) has studied the reaction of various chemical substances in *Oedogonium*. He finds that benzidine and tolidine have a negative reaction on oxidases and peroxidases in *Oe. capillare* (L.) Kütz., but secures color reactions in other species of the genus. The polyphenols produce definite coloring in *Oe. capillare*, and incidentally in some species of *Cladophora*. In other species of *Oedogonium* the polyphenol solution remains unchanged or becomes brown instead of assuming a reddish-brown or bluish-gray to black color, as is the result in many algae. Prát (72) also reports that species of *Oedogonium* vary greatly in both the speed and the intensity of their reactions to Schiff's reagent.

Massa (56) could detect no ascorbic acid and neither oxidases nor peroxidases in species of *Oedogonium*. Yamaha and Ueda (116), using various buffers, exposed several kinds of plants to solutions of different pH values. Susceptibility was gauged by protoplasmic streaming and evidence of plasmolysis. The se-

quence representing the resistance to free H-ions in all buffer treatments was *Elodea* > *Hydrodictyon* > *Oedogonium* > *Spirogyra* > *Oscillatoria*.

ALGAL CULTURES

For many years biologists have maintained growth of certain algae in the laboratory in lake or pond water "in a north window" for considerable lengths of time. Many features of development and reproduction in the algae were elucidated in such "cultures". In the last several decades phycologists have made enormous strides in the culture of all sorts of algae in specially prepared solutions under special conditions of pH, temperature, light intensity and composition of media. Some, perhaps most, algae have remarkably specific requirements for best growth, while others appear to be more cosmopolitan in their requirements. E. G. Pringsheim (78) pioneered in the culturing of many kinds of algae with special requirements for growth. His culture collections or many of their descendants are now in the Botany School at the University of Cambridge, England, available for research. The Culture Collections of Algae in the Department of Botany, Indiana University, Bloomington, Indiana (U.S.A.), under the able supervision of Dr. R. C. Starr are also being maintained for research (as well as for classroom use). Here also many kinds of algae authoritatively named are kept in constant stock, and cultures may be had at small cost. Both of these institutions maintain pure cultures of both male and female filaments of *Oedogonium cardiacum* Wittr. It is to be hoped that additional species of the Oedogoniaceae will soon be available.

ACKNOWLEDGMENT

The writer wishes to express his best thanks to Dr. Theodor Just for putting at his disposal the library facilities of the Chicago Natural History Museum, and also of the staff of Deering Library of Northwestern University for many courtesies.

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